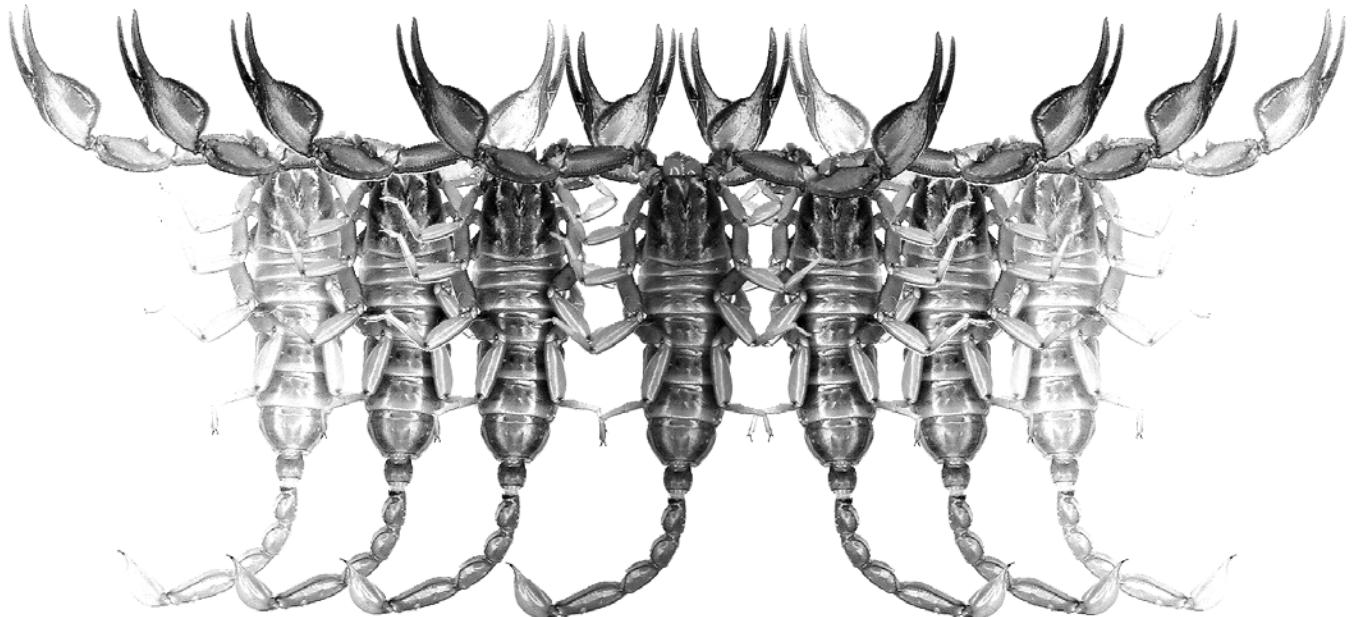


# *Euscorpius*

Occasional Publications in Scorpiology



**A New Trichobothrial Character for the High-Level  
Systematics of Buthoidea (Scorpiones: Buthida)**

**Victor Fet, Michael E. Soleglad and Graeme Lowe**

**July 2005 – No. 23**

# *Euscorpius*

## Occasional Publications in Scorpiology

*EDITOR:* Victor Fet, Marshall University, ‘[fet@marshall.edu](mailto:fet@marshall.edu)’

*ASSOCIATE EDITOR:* Michael E. Soleglad, ‘[soleglad@la.znet.com](mailto:soleglad@la.znet.com)’

*Euscorpius* is the first research publication completely devoted to scorpions (Arachnida: Scorpiones). *Euscorpius* takes advantage of the rapidly evolving medium of quick online publication, at the same time maintaining high research standards for the burgeoning field of scorpion science (scorpiology). *Euscorpius* is an expedient and viable medium for the publication of serious papers in scorpiology, including (but not limited to): systematics, evolution, ecology, biogeography, and general biology of scorpions. Review papers, descriptions of new taxa, faunistic surveys, lists of museum collections, and book reviews are welcome.

### **Derivatio Nominis**

The name *Euscorpius* Thorell, 1876 refers to the most common genus of scorpions in the Mediterranean region and southern Europe (family Euscorpiidae).

*Euscorpius* is located on Website ‘<http://www.science.marshall.edu/fet/euscorpius/>’ at Marshall University, Huntington, WV 25755-2510, USA.

---

The International Code of Zoological Nomenclature (ICZN, 4th Edition, 1999) does not accept online texts as published work (Article 9.8); however, it accepts CD-ROM publications (Article 8). *Euscorpius* is produced in two *identical* versions: online (ISSN 1536-9307) and CD-ROM (ISSN 1536-9293). Only copies distributed on a CD-ROM from *Euscorpius* are considered published work in compliance with the ICZN, i.e. for the purposes of new names and new nomenclatural acts. All *Euscorpius* publications are distributed on a CD-ROM medium to the following museums/libraries:

- **ZR**, Zoological Record, York, UK
- **LC**, Library of Congress, Washington, DC, USA
- **USNM**, United States National Museum of Natural History (Smithsonian Institution), Washington, DC, USA
- **AMNH**, American Museum of Natural History, New York, USA
- **CAS**, California Academy of Sciences, San Francisco, USA
- **FMNH**, Field Museum of Natural History, Chicago, USA
- **MCZ**, Museum of Comparative Zoology, Cambridge, Massachusetts, USA
- **MNHN**, Museum National d'Histoire Naturelle, Paris, France
- **NMW**, Naturhistorisches Museum Wien, Vienna, Austria
- **BMNH**, British Museum of Natural History, London, England, UK
- **MZUC**, Museo Zoologico “La Specola” dell’Universita de Firenze, Florence, Italy
- **ZISP**, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia
- **WAM**, Western Australian Museum, Perth, Australia
- **NTNU**, Norwegian University of Science and Technology, Trondheim, Norway

# A new trichobothrial character for the high-level systematics of Buthoidea (Scorpiones: Buthida)

Victor Fet<sup>1</sup>, Michael E. Soleglad<sup>2</sup> and Graeme Lowe<sup>3</sup>

<sup>1</sup> Department of Biological Sciences, Marshall University, Huntington, WV 25755-2510, USA

<sup>2</sup> P. O. Box 250, Borrego Springs, California 92004, USA

<sup>3</sup> Monell Chemical Senses Center, 3500 Market St., Philadelphia, PA 19104-3308, USA

---

## Summary

The high-level systematics and phylogeny of the scorpion superfamily Buthoidea are unresolved. A new, formerly undetected character is reported here: the relative alignment of  $d_3$  trichobothrium and  $DM_c$  carina on the pedipalp patella. This and other characters are discussed in the context of possible high-level divisions of Buthoidea. Based on this analysis, we suggest a breakdown of Buthoidea into six proposed tentative phylogenetic groups: ***Buthus*** group, ***Ananteris*** group, ***Isometrus*** group, ***Charmus*** group, ***Uroplectes*** group, and ***Tityus*** group.

---

## Introduction

The high-level systematics and phylogeny of the scorpion superfamily Buthoidea are unresolved (Soleglad & Fet, 2003b; Coddington et al., 2004). The superfamily currently includes 88 valid genera of extant and fossil scorpions, among them a number of genera containing the most toxic known scorpion species. The monophyly of Buthoidea (the only superfamily of parvorder Buthida) is well demonstrated; among many other character sets, it is supported by so-called trichobothrial type A (Vachon, 1974; Soleglad & Fet, 2001, 2003b). However, the relationship between two buthoid families, Buthidae and Microcharmidæ, remains unclear (Fet, 2000; Soleglad & Fet, 2003b).

Fet & Lowe (2000) discussed the historical attempts to recognize subfamilies in Buthidae using a limited set of various diagnostic characters (Kraepelin, 1899, 1905; Birula, 1917a, 1917b, etc.). Currently, subfamilies in Buthidae are not recognized (Stahnke, 1972; Sissom, 1990; Fet & Lowe, 2000) since there is no consensus about the diagnostic criteria.

Vachon (1975) introduced a new character for high-level systematics of Buthidae, which separates all Buthoidea into two groups, *alpha* and *beta*, according to the mutual position of trichobothria  $d_1-d_3-d_4$  on the dorsal aspect of pedipalp femur, and in part, the surface location of trichobothrium  $d_2$ . This grouping did not correspond to any of the subfamily subdivisions proposed by the earlier authors.

Here, we report a new, formerly undetected character: the relative position of  $d_3$  trichobothrium and dorsomedian carina ( $DM_c$ ) on the pedipalp patella. The importance of the  $DM_c$  carina as a synapomorphy of Buthoidea was demonstrated by Soleglad & Fet (2003b) and was used recently as the primary character for the placement of fossil scorpion *Uintascorpio* in family Buthidae (Santiago-Blay et al., 2004b). However, the position of patellar trichobothria has not been sufficiently studied so far. In relation to the  $DM_c$  carina, trichobothrium  $d_3$  can be located internally (i.e. between the dorsointernal ( $DI_c$ ) and  $DM_c$  carinae) or externally (i.e. between the  $DM_c$  and dorsoexternal ( $DE_c$ ) carinae). The distribution of the new character appears to split all genera of Buthoidea in two major groups. Below, we provide the first comparative study of this character as it relates to the *alpha/beta* pattern in Buthoidea and discuss its phylogenetic implications.

Based on the cladistic analysis presented in this paper, we propose six tentative phylogenetic groupings within the superfamily Buthoidea: ***Buthus*** group, ***Ananteris*** group, ***Isometrus*** group, ***Charmus*** group, ***Uroplectes*** group, and the ***Tityus*** group. (The bold font is used here and elsewhere in this paper solely for better visual comprehension, not because we assign to it any official taxonomic value). Individual genus placements within these six groups are stated in Table 1 where they are correlated with the characters discussed in this paper. As will be shown, these six hypothesized phylogenetic groups of buthoids and their interrelationships are delineated, in part, by the small set of fundamental char-

ters discussed in this paper. Although predictively, these groups are not completely defined by the small character set presented herein, we believe they do in fact represent a reasonable partitioning of Recent buthoid scorpions and will, in our opinion, further enhance future discussions involving the systematics of this highly complicated group. The small set of characters and information on biogeographical associations of these six buthoid groups are provided below.

## Methods & Material

### Terminology and conventions

Terminology describing pedipalp chelal ornamentation follows that described and illustrated in Soleglad & Sissom (2001). Terminology for the pedipalp patella follows that described in Soleglad & Fet (2003b). Terminology for the orthobothrioxic types follows that described in Vachon (1974) and Soleglad & Fet (2001), and terminology for the sternum is that of Soleglad & Fet (2003a).

Note, as stated above, we follow the designations of buthoid trichobothria as established by Vachon (1974); however, we follow homology of these trichobothria across orthobothrioxic types as established by Soleglad & Fet (2001). It is important to note that in Soleglad & Fet (2001: 9–10), different designations were employed in some cases in order to emphasize suggested trichobothrium homology between fossil and Recent scorpions, but, as these authors stated, the purpose was not to consolidate and/or change the accepted designations as originally established by Vachon (1974).

### Cladistic analysis software packages

Software package PAUP\* Version 4 (beta) (Swofford, 1998) was used for Maximum Parsimony (MP) analysis of morphology-based character codings. Cladograms from PAUP\* were generated by TreeView (Win 32) Version 1.5.2 (Page, 1998).

### Abbreviations

**List of depositories:** AMNH, American Museum of Natural History, New York, New York, USA; CAS, California Academy of Sciences, San Francisco, California, USA; GL, Personal collection of Graeme Lowe, Philadelphia, Pennsylvania, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MES, Personal collection of Michael E. Soleglad, Borrego Springs, California, USA; MHNG, Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland; NMB, Naturhistorisches Museum

Basel, Basel, Switzerland; USNM, United States National Museum, Smithsonian Institution, Washington, DC, USA; VF, Personal collection of Victor Fet, Huntington, West Virginia, USA; WDS, Personal collection of W. David Sissom, Texas, USA; ZMH, Zoologisches Museum Hamburg, Hamburg, Germany.

### Material examined

The following buthoid material was examined for analysis and/or illustrations provided in this paper. Refer to this section for locality and gender data of species-level illustrations.

**Buthidae:** *Alayotityus nanus* Armas, 1973, Santiago, Cuba, (VF); *Androctonus bicolor* Ehrenberg, 1828, Lhav, Israel, ♂ (MES); *Androctonus crassicauda* (Olivier, 1807), Duhai, Oman, ♂ (GL); *Anomalobuthus rickmersi* Kraepelin, 1900, Bukhara, Uzbekistan, ♂♀ (VF); *Apistobuthus pterygocercus* Finnegan, 1932, Oman, (VF); *Buthacus yotvatensis* Levy, Amitai & Shulov, 1973, Abu Dhabi, United Arab Emirates, ♂ (VF); *Butheolus anthracinus* (Pocock, 1897), Dhofar, Oman, ♂ (GL); *Butheolus gallagheri* Vachon, 1980, Oman, ♂ (GL); *Butheolus thalassinus*, Ta’izz, Yemen, ♂ (WDS); *Buthus occitanus* Amoreux, 1789, Casablanca, Morocco, (MES); *Centruroides bicolor* (Pocock, 1898), Quepos, Costa Rica, ♂ (GL); *Centruroides elegans* (Thorell, 1876), Ixtapan, Guerrero, Mexico, ♀ (MES); *Centruroides exilicauda* (Wood, 1863), Cabo San Lucas, Baja California Sur, Mexico, ♀ (MES); *Centruroides hentzi* (Banks, 1910), Panama City, Florida, USA, ♀ (MES); *Centruroides infamatus ornatus* Pocock, 1902, Tamazula, Jalisco, Mexico, ♀ (MES); *Centruroides koesteri* Kraepelin, 1911, Puntarenas, Costa Rica, ♀ (GL); *Centruroides limbatus* (Pocock, 1898), Limon, Costa Rica, ♀ (GL); *Centruroides limpidus* (Karsch, 1879), Oaxtepec, Morelos, Mexico, ♀ (GL); *Centruroides margaritatus* (Gervais, 1841), Panama, ♂ (MES); *Centruroides nigrescens* (Pocock, 1898), Oaxaca, Mexico, ♂♀ (GL); *Centruroides nigrovariatus baergi* Hoffmann, 1932, Tehuacan, Puebla, Mexico, ♀ (MES); *Centruroides noxius* Hoffmann, 1932, Tepic, Nayarit, Mexico, ♀ (MES); *Centruroides pallidiceps* Pocock, 1902, Mazatlan, Sinaloa, Mexico, ♀ (MES); *Centruroides sculpturatus* Ewing, 1928, Caborca, Sonora, Mexico, ♀ (MES); *Centruroides vittatus* (Say, 1821), Cuatro Cienegas, Coahuila, Mexico, ♂ (MES); *Compsobuthus acutecarinatus* (Simon, 1882), Oman, ♀ (GL); *Compsobuthus brevimanus* (Werner, 1936), Sana'a, Yemen, ♂ (WDS); *Compsobuthus maindroni* (Kraepelin, 1900), Hajar al Sharqi, Oman, ♀ (GL); *Compsobuthus matthieseni* (Birula, 1905), Baghdad, Iraq, (VF); *Compsobuthus polisi* Lowe, 2001, Wadi Dirif, Oman, holotype ♂ (NMB); *Compsobuthus rugosulus* (Pocock, 1900), Tatta,

	$d_3/DM_c$	$DM_c/d_3$			
	Beta	Beta		Alpha	
	$d_2(d)$	$d_2(d)$	$d_2(i)$	$d_2(d)$	$d_2(i)$
<b><i>Buthus</i> group (39 genera)</b>					
<i>Androctonus, Anomalobuthus, Apistobuthus, Baloorthochirus, Birulatus, Buthacus, Butheolus, Buthiscus, Buthus, Cicileus, Compsobuthus, Congobuthus, Darchenia, Hemibuthus, Hottentotta, Iranobuthus, Kraepelinia, Lanzatus*, Leiurus, Liobuthus*, Lissothus<sup>1</sup>, Mesobuthus, Microbuthus<sup>1</sup>, Neobuthus, Odontobuthus, Orthochiroides, Orthochirus<sup>2</sup>, Paraorthochirus, Pectinibuthus*, Plesiobuthus*, Polisius, Psammobuthus, Razianus, Sabinebuthus*, Sassanidothus, Simonoides, Somalibuthus, Vachoniolus*, Vachonus</i>	X				
<b><i>Ananteris</i> group (6 genera)</b>					
<i>Akentrobuthus*, Ananteris, Himalayotityobuthus, Lychas, Lychasioides, Microananteris</i>		X			
<b><i>Isometrus</i> group (7 genera)</b>					
<i>Afroisometrus*, Australobuthus, Babycurus, Hemilychas, Isometroides, Isometrus*, Odonturus</i>			X		
<b><i>Charmus</i> group (3 genera)</b>					
<i>Charmus, Somalicharmus, Thaicharmus</i>					X
<b><i>Uroplectes</i> group (18 genera)</b>					
<i>Ankaranocharmus<sup>1</sup>, Butheoloides, Buthoscorpio, Egyptobuthus, Grosphus, Karasbergia<sup>1</sup>, Microcharmus, Neogrosphus, Neoprotobuthus, Palaeogrosphus, Parabuthus, Pseudolishthus, Pseudolychas, Pseudouroplectes, Tityobuthus, Troglotityobuthus, Uroplectes, Uroplectoides</i>					X
<b><i>Tityus</i> group* (9 genera)</b>					
<i>Alayotityus<sup>1</sup>*, Centruroides*, Mesotityus*, Microtityus<sup>2</sup>*, Ropalurus*, Tityopsis*, Tityus*, Troglorhopalurus*, Zabius<sup>1</sup>*</i>					X

**Table 1:** Fundamental trichobothrial pattern characters for superfamily Buthoidea (82 Recent genera) partitioned into six groups: patellar  $d_3$  position with respect to dorsomedian ( $DM_c$ ) carina (i.e., internal or external to carina); and femoral alpha/beta pattern with special emphasis on the position of trichobothrium  $d_2$  (i.e., dorsal surface or internal surface). (d) = dorsal surface of femur; (i) = internal surface of femur. \* Tibial spurs absent; <sup>1</sup> Femur trichobothrium  $d_2$  absent, or, <sup>2</sup>  $d_2$  vestigial to absent.

Pakistan, ♀ (CAS); *Compsobuthus wernerii* (Birula, 1908), Dintorni di Ju Amlah, Yemen, ♀ (WDS); *Grosphus hirtus* Kraepelin, 1901, Tamatave Province, Perinet, Madagascar, ♀ (MES); *Grosphus madagascariensis* (Gervais, 1843), Anjro, Madagascar, ♂ (GL); *Hottentotta hottentotta* (Fabricius, 1787), North Province, Cameroon, ♀ (GL); *Hottentotta jayakari* (Pocock, 1895), between Seeb & Al Khod, Oman, ♂ (GL); *Hottentotta judaicus* (Simon, 1872), Jerusalem, Israel, ♀ (MCZ); *Hottentotta minax* (L. Koch, 1875), Eritrea, ♂ (VF); *Hottentotta trilineatus* (Peters, 1861), S. Magadi, Kenya, ♂ (GL); *Isometroides vescus* (Karsch, 1880), South Australia, Australia, ♀ (GL); *Isometrus maculatus* (DeGeer, 1778), Diego Garcia, Indian Ocean, (MES), Honolulu Co., Hawaii, USA, ♀ (GL); *Isometrus melanodactylus* (L. Koch, 1867), New South Wales, Australia, ♂ (GL); *Isometrus* sp., Papua New Guinea, ♀ (MES); *Kraepelinia palpator* (Birula, 1903), Badghyz, Turkmenistan, ♀ (VF); *Leiurus quinquestriatus* (Ehrenberg,

1828), Saudi Arabia, (VF); *Liobuthus kessleri* Birula, 1898, Chardara, Kazakhstan, ♀ (VF); *Lychas marmoreus*, South Australia, Australia, ♂ (GL); *Lychas* sp., Viti Levu, Fiji, ♀ (MES); *Lychas* sp., Indonesia, (VF); *Mesobuthus caucasicus* (Nordmann, 1840), Chardara, Kazakhstan, ♀ (VF); *Microbuthus* sp., Rusail, Oman, ♂ (GL); *Odontobuthus doriae* (Thorell, 1877), Kachan, Iran, ♀ (CAS); *Odontobuthus odonturus* (Pocock, 1897), Indus delta, Pakistan, ♀ (AMNH); *Orthochirus scrobiculosus* (Grube, 1873), Israel, (MES); *Parabuthus granulatus* (Ehrenberg, 1831), Rehoboth, RSA, ♂ (GL); *Parabuthus liosoma* (Ehrenberg, 1828), Sodora, Ethiopia, ♂ ♀ (GL); *Parabuthus pallidus* Pocock, 1895, Lodwar Kenya, ♀ (GL); *Parabuthus transvaalicus* Purcell, 1899, Beitbridge, Zimbabwe, ♂ (GL); *Parabuthus* sp., Kenya, ♀ (VF); *Paraorthochirus glabrifrons* (Kraepelin, 1903), Muscat, Oman, holotype (ZMH); *Polisius persicus* Fet, Capes & Sissom, 2001, Zahedan, Iran, ♂ (USNM); *Razianus zarudnyi* (Birula, 1903), Gachsaran,

Fars, Iran, (VF); *Rhopalurus junceus* (Herbst, 1800), Camaquey, Sibanidi, Cuba, ♀ (VF); *Tityus championi* Pocock, 1898, Puntarenas, Costa Rica, ♂ (GL); *Tityus dedoslargos* Francke et Stockwell, 1987, Quepos, Costa Rica, ♂♀ (GL); *Tityus ecuadorensis* Kraepelin, 1896, Vilcabamba, Ecuador, ♂ (GL); *Tityus nematochirus* Mello-Leitão, 1940, Bucaramango, Colombia, ♂ (MES); *Tityus ocelote* Francke et Stockwell, 1987, Quepos, Costa Rica, ♂ (GL); *Uroplectes planimanus* (Karsch, 1879), Maun, Botswana, ♂ (GL); *Uroplectes vittatus* (Thorell, 1876), Doddiebum, Zimbabwe, ♂ (VF), Nata, Botswana, ♀ (GL).

**Microcharmidæ:** *Microcharmus hauseri* Lourenço, 1996, Lokobe Natural Reserve, Île Nosy Be, Madagascar, holotype ♂ (MHNG).

## Character Analysis

Soleglad & Fet (2003b), in their high-level analysis of Recent scorpion systematics, established the dorsomedian ( $DM_c$ ) carina of the pedipalp patella as a synapomorphy for parvorder Buthida. In the same analysis, they expanded the definition of the important femoral trichobothria arrangement, *alpha/beta*, as originally established by Vachon (1975). In this paper, we expand further on these two character structures and, for the first time, present an important new character, the arrangement of the patellar dorsal trichobothria  $d_1-d_5$ , in particular, trichobothrium  $d_3$ , as they relate to the  $DM_c$  carina.

**$DM_c$  carina.** Vachon (1952: Figs. 66–68) illustrated eight carinae for the pedipalp patella in his section on scorpion morphology nomenclature. Based on the analysis of Soleglad & Fet (2000b: 52–58), it turned out that these eight carinae (the largest number of carinae occurring on the patella in any known Recent scorpion) applied to the buthoids *only*, in particular, the dorsomedian ( $DM_c$ ) carina which is unique to the buthoids. In Vachon's (1952) analysis, the overwhelming majority of taxa described were buthoids (the only other scorpions discussed were *Euscorpius* (superfamily Chactoidea) and *Scorpio* (superfamily Scorpionoidea)), therefore this unique carina, termed “médiane dorsale”, was included in Vachon's nomenclature.

Santiago-Blay et al. (2004b: Fig. 5–7) used the  $DM_c$  carina as the primary character for placing the Eocene fossil scorpion *Uintascorpio halandrasorum* Perry, 1995 in the family Buthidae. In this paper Santiago-Blay et al. (2004b: 8) further verified the existence of the  $DM_c$  carina for 32 extant buthoid genera based on specimen examination, roughly 40 % of all currently described genera. In this paper, based on existing literature, 20 additional buthoid genera were verified as having the  $DM_c$  carina, bringing the total to 52 genera, 63 % of described Recent buthoid genera. It must be noted here,

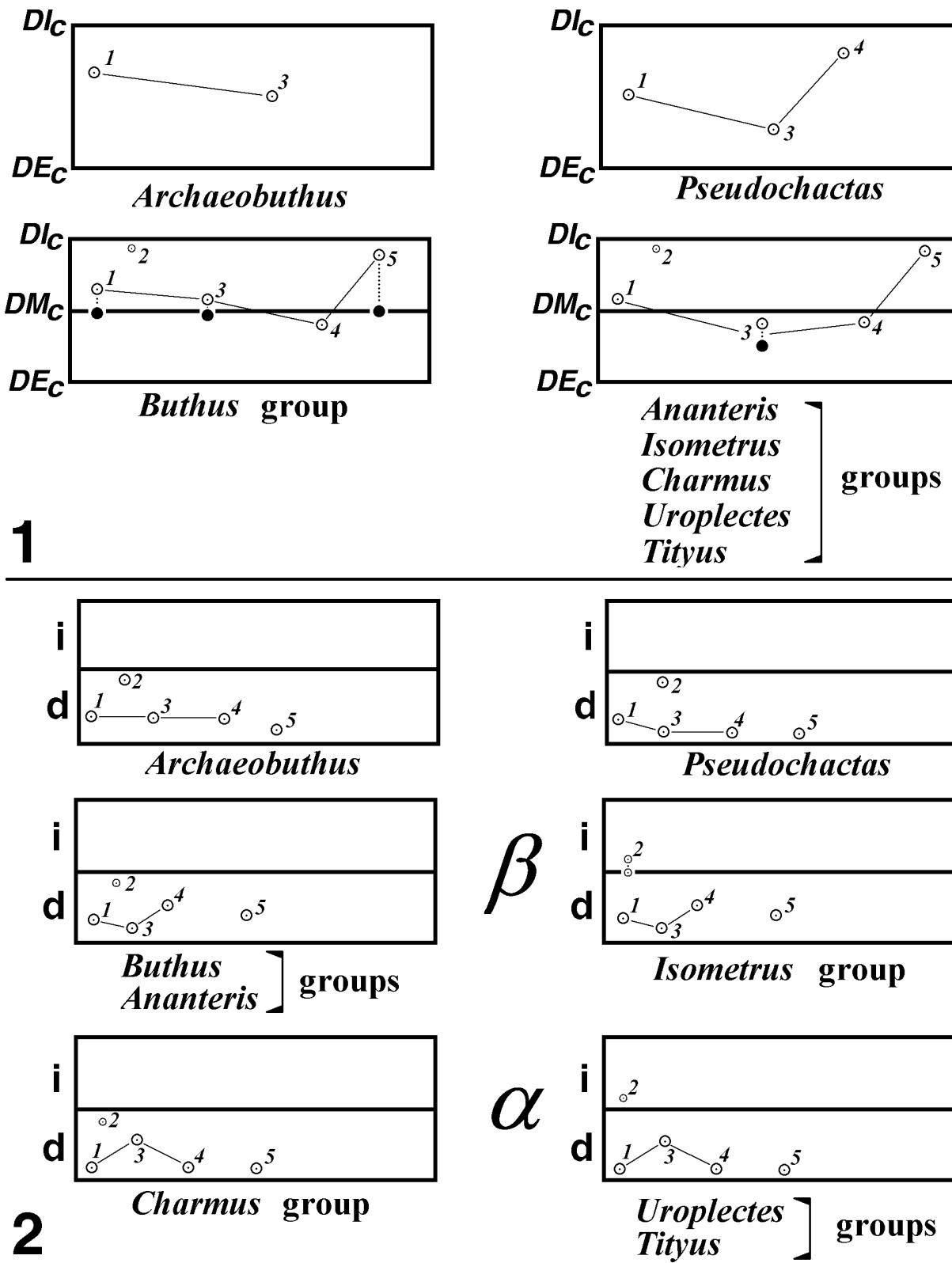
however, that not all authors necessarily illustrated the  $DM_c$  carina, especially if it is somewhat smooth in its structure, or in cases where carinae were not illustrated at all. Therefore, we suspect that in the remaining genera which could not be verified, many will prove to have this unique carina.

Soleglad & Fet (2003b) established that outgroup taxon *Pseudochactas ovchinnikovi* (Pseudochactidae) does not have the  $DM_c$  carina (Fig. 3). They hypothesized that the Carboniferous family Palaeopisthacanthidae also lacked this carina, based on a partial description of the patella of fossil scorpion *Compsoscorpius elegans* by Jeram (1994b); i.e., they exhibited the *seven carinae configuration*, hypothesized as primitive for Recent scorpions. In the same analysis, Soleglad & Fet (2003b) stipulated that the outgroup species *Archaeobuthus estephani* exhibited this unique carina, based entirely on the figure provided by Lourenço (2001b: Fig. 13). However, after a recent reanalysis of the type specimen (Santiago-Blay et al., in preparation) we have concluded that the existence of the  $DM_c$  carina in *Archaeobuthus* cannot be determined one way or the other. We discuss this further in the section on cladistic analysis.

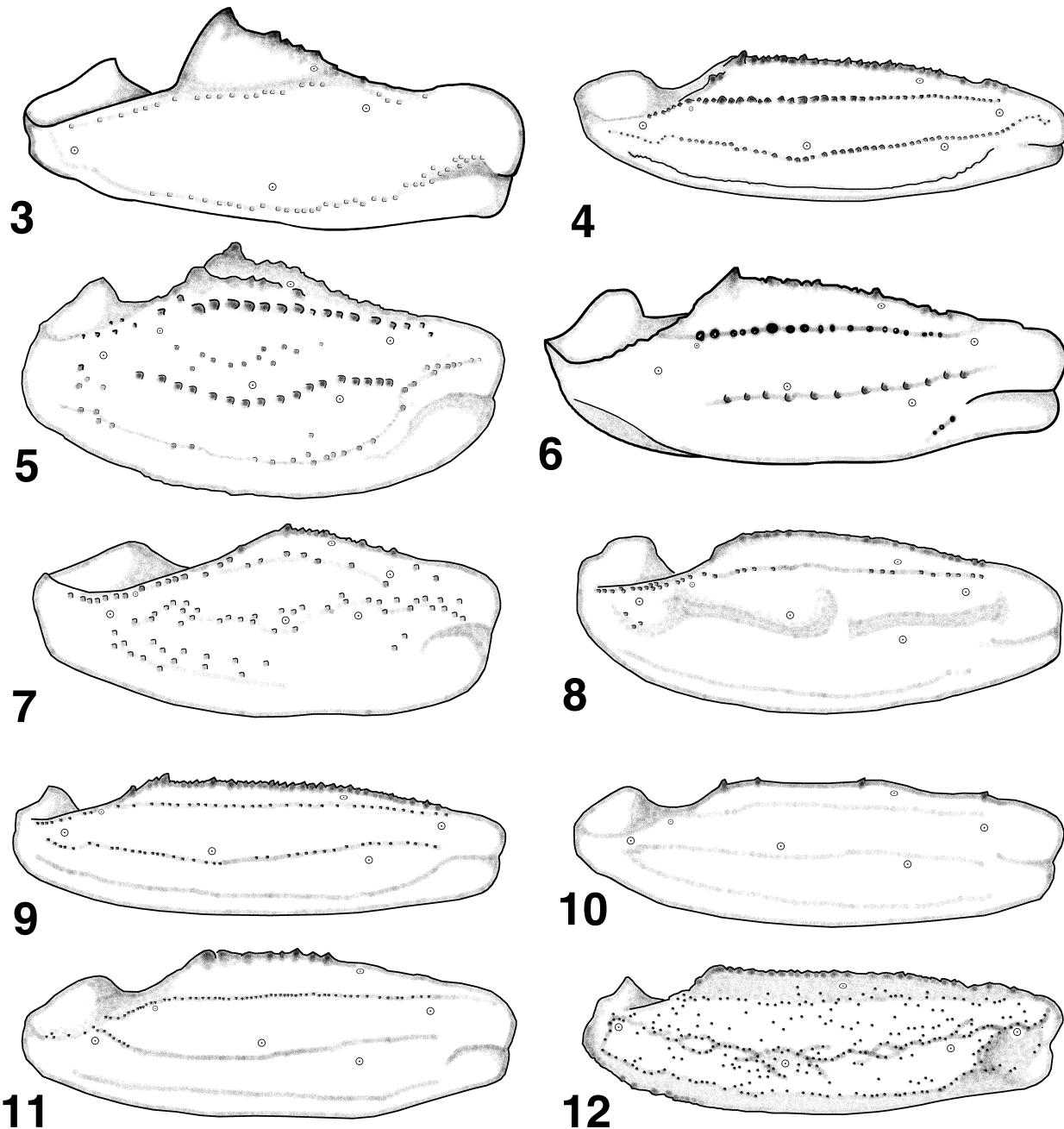
**$DM_c$  and trichobothrium  $d_3$  alignment.** Vachon (1974: Figs. 30–36) defined the orthobothrioxic Type A trichobothrial pattern for the buthoids. This pattern is a major synapomorphy for the parvorder Buthida (Soleglad & Fet, 2003b), as are the other fundamental patterns established by Vachon (1974) for other high-level Recent scorpion groups (i.e., Type B, parvorder Chaerilida; Type C, parvorder Iurida; and Type D, parvorder Pseudochactida, the latter orthobothrioxic type defined by Soleglad & Fet, 2001: Fig. 13). In the Type A pattern, we find five dorsal trichobothria located on the patella,  $d_1-d_5$ , with trichobothrium  $d_2$  being petite in size.

In a detailed analysis of the patella of Recent buthoid genera, including available specimens and the ample volume of existing literature, we were able to confirm two basic alignments of the dorsal patellar trichobothria as they relate to the  $DM_c$  carina: trichobothrium  $d_3$  is positioned on the dorsal surface either “internally” (i.e., between the dorsointernal ( $DI_c$ ) and  $DM_c$  carinae), or it is located “externally” (i.e., between the  $DM_c$  and dorsoexternal ( $DE_c$ ) carinae). That is, the  $DM_c$  carina horizontally bisects the dorsal surface of the patella. In general, this orientation is *consistent* within a genus and, as important, the collection of genera compliant to these two  $d_3-DM_c$  arrangements are congruent to the *alpha/beta* pattern as defined by Vachon (1975). That is, this character is important phylogenetically, which we discuss in detail in the **Cladistic analysis** section below.

Figure 1 shows four configurations of the patellar dorsal trichobothrial patterns as they relate to the dorsal carinae. The two outgroup taxa, *Archaeobuthus* and *Pseudochactas*, exhibit a subset of the Type A dorsal



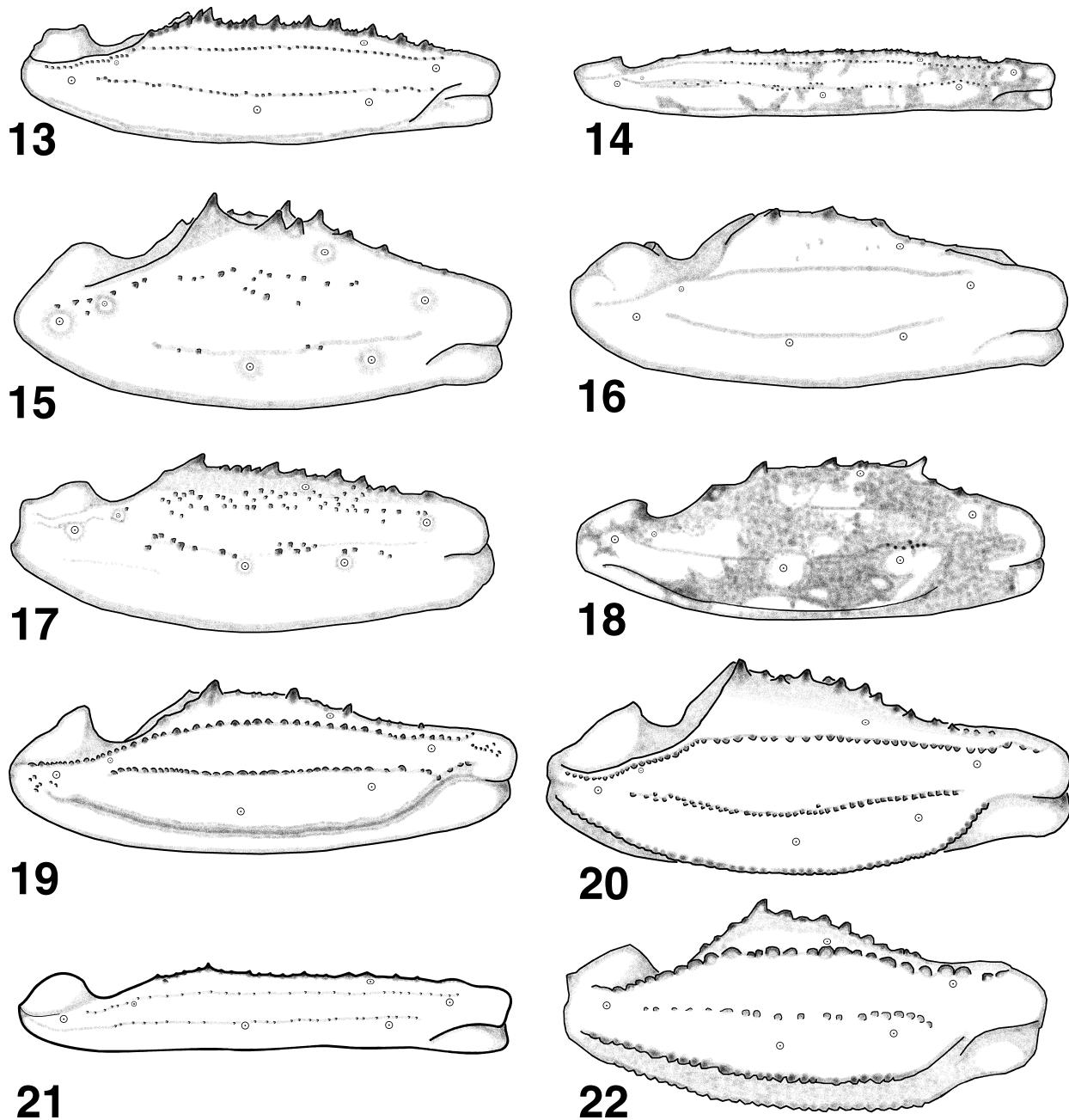
**Figures 1-2:** Schematic diagram of pedipalp patella (dorsal surface) and femur (dorsal and internal surfaces) illustrating important trichobothrial arrangements. **1.** Patella. Note, closed circles depict alternative positions for indicated trichobothria as follows: *Microbuthus* in *Buthus* group (lower left) and *Tityus* group (lower right).  $DI_c$  = dorsointernal carina,  $DM_c$  = dorsomedian carina,  $DE_c$  = dorsoexternal carina. **2.** Femur. i = internal, d = dorsal;  $\alpha$  = alpha,  $\beta$  = beta.



**Figures 3-12:** Pedipalp patella, dorsal view, showing the alignment of trichobothrium  $d_3$  with respect to the dorsomedian ( $DM_c$ ) carina. In the buthoid figures  $d_3$  is situated *internal* to or *on* the  $DM_c$  carina. **3.** *Pseudochactas ovchinnikovi* (after Soleglad & Fet, 2003b, in part). Note,  $DM_c$  carina is absent as well as trichobothria  $d_2$  and  $d_4$ . **4.** *Androctonus bicolor*. **5.** *Razianus zarudnyi*. **6.** *Mesobuthus caucasicus* (after Soleglad & Fet, 2003b, in part). **7.** *Liobuthus kessleri*. **8.** *Orthochirus scrobiculosus*. **9.** *Compsobuthus matthiesseni*. **10.** *Anomalobuthus rickmersi*. **11.** *Buthacus yotvatensis*. **12.** *Microbuthus* sp. Note, trichobothrium  $d_3$  bifurcates the  $DM_c$  carina and trichobothrium  $d_2$  is absent. Only trichobothrium  $i$  and  $d_1-d_5$  are shown in these figures.

trichobothria, their hypothesized homology with the buthoid Type A pattern being based on Soleglad & Fet (2001: Fig. 3). Also, in the two outgroups, the  $DM_c$  carina is depicted as absent (Figs. 1 and 3). For the buthoids, two configurations are distributed across the six proposed groups of genera as follows:

Exclusively in the ***Buthus*** group, the trichobothrium  $d_3$  is located internally on the dorsal surface (rarely positioned on the  $DM_c$  carina, see *Liobuthus* and *Microbuthus* below); this accounts for no less than 39 genera. In this pattern only trichobothrium  $d_4$  is consistently located externally on the surface. Figs. 4–12 illustrate this



**Figures 13–22:** Pedipalp patella, dorsal view, showing the alignment of trichobothrium  $d_3$  with respect to the dorsomedian ( $DM_c$ ) carina. In these figures,  $d_3$  is situated external to the  $DM_c$  carina. **13.** *Lychas* sp. **14.** *Isometrus maculatus*. **15.** *Grosphus hirtus*. **16.** *Parabuthus* sp. **17.** *Uroplectes vittatus*. **18.** *Microcharmus hauseri*, holotype. **19.** *Centruroides margaritatus* (after Santiago-Blay et al., 2004b, in part). **20.** *Rhopalurus junceus* (after Santiago-Blay et al., 2004b, in part). **21.** *Tityus nematochirus* (after Soleglad & Fet, 2003b, in part). **22.** *Alayotityus nanus* (note trichobothrium  $d_2$  is absent). Only trichobothria  $i$  and  $d_1-d_5$  are shown in these figures.

pattern for nine major genera in the *Buthus* group. These figures show various degrees of development of the  $DM_c$  carina, from a well delineated crenulate carina in genera *Androctonus* (Fig. 4), *Razianus* (Fig. 5), *Mesobuthus* (Fig. 6) and *Compsobuthus* (Fig. 9); to irregularly defined as in *Orthochirus* (Fig. 8), *Liobuthus*

(Fig. 7) and *Microbuthus* (Fig. 12); and to weak or smooth as in genera *Anomalobuthus* (Fig. 10) and *Buthacus* (Fig. 11). The alignment of the dorsal trichobothria in genus *Microbuthus* (Figs. 1, 12; Vachon, 1952: Figs. 470, 471; Lourenço, 2002: Fig. 16) is very interesting: we see  $d_1$ ,  $d_3$ ,  $d_4$  and  $d_5$  are found either on or

external to the  $DM_c$  carina. In particular,  $d_3$  (Fig. 12, Lourenço, 2002: Fig. 16) is sometimes located in a “dimple” bifurcating, in part, the  $DM_c$  carina. In many buthoids exhibiting an internally placed  $d_3$ , we see that the  $DM_c$  carina angles externally somewhat at the position of  $d_3$ ’s location (e.g., Figs. 4, 5, 7, 8, and 9). In particular,  $d_3$  in *Liobuthus* (Fig. 7) is located in a dimple bifurcating the  $DM_c$  carina, similar to that seen in *Microbuthus*. The placement of trichobothrium  $d_5$  in *Microbuthus* is unprecedented in the buthoids. This placement appears to be caused, in part, by the internal tapering of the  $DM_c$  carina at the distal aspect of the patella, a little more exaggerated than that seen in other genera; but we also note that  $d_5$  is not positioned as close to the dorsointernal ( $DI_c$ ) carina as in other genera exhibiting either  $d_3$ - $DM_c$  alignment. Finally, the unique configuration exhibited in *Microbuthus* may also be the product of the  $DM_c$  carina slightly repositioning in an internal direction on the patellar surface. This hypothesis is further supported by the inline to external position of trichobothria  $d_1$ ,  $d_3$  and  $d_5$  with respect to the  $DM_c$  carina.

In the other five groups of genera, *Ananteris*, *Isometrus*, *Charmus*, *Uroplectes* and *Tityus* (comprising 43 genera), the trichobothrium  $d_3$  is positioned externally on the dorsal surface. Figures 13–22 illustrate this pattern for four of the five groups complying to this pattern (members of the *Charmus* group were not available). In these figures are included the genus *Microcharmus* (Fig. 18), presently assigned to family Microcharmidæ; *Lychas* (Fig. 13), a member of the *Ananteris* group; *Isometrus* (Fig. 14), member of the *Isometrus* group; plus genera from the *Uroplectes* and *Tityus* groups. In this pattern, two trichobothria,  $d_3$  and  $d_4$ , are situated external to this carina. As in the *Buthus* group, one can observe different degrees of development in the  $DM_c$  carina: well developed and granulate as in genera *Lychas* (Fig. 13), *Isometrus* (Fig. 14), *Uroplectes* (Fig. 17), and the four members of the *Tityus* group; and smooth and/or irregular as in genera *Grosphus* (Fig. 15), *Parabuthus* (Fig. 16), and *Microcharmus* (Fig. 18). In the *Tityus* group, the trichobothrium  $d_3$  is located more external from the  $DM_c$  carina than the other groups (Fig. 1). In three of the four genera illustrated for the *Tityus* group, we see that trichobothrium  $d_3$  is located considerably external to the  $DM_c$  carina. Note that for the species *Tityus nematochirus* (Fig. 21),  $d_3$  is situated quite close to this carina, but we attribute this to the extreme slenderness of the species. In other *Tityus* species illustrated in the literature,  $d_3$  is positioned as illustrated here for genera *Centruroides* (Fig. 19), *Rhopalurus* (Fig. 20), and *Alayotityus* (Fig. 22).

We also see other tendencies in trichobothria positions on the patella as it relates to the two alignments of  $d_3$ : in the *Buthus* group trichobothrium  $d_1$  is located slightly internal to the  $DM_c$  carina whereas in the other

alignment,  $d_1$  is located roughly inline with  $DM_c$ . In the *Buthus* group, the  $d_1$ - $d_3$ - $d_4$  juncture is either formed in a straight line, or angles upward towards the  $DI_c$  carina, whereas in the other alignment, the  $d_1$ - $d_3$ - $d_4$  juncture angles downward towards the  $DE_c$  carina. In both configurations, trichobothrium  $d_4$  is located external to  $DM_c$ .

The assignment of the genera to the two  $d_3$ - $DM_c$  alignments is based on the analysis of actual specimens as well as illustrations in available literature. For actual specimens, the representatives of five out of six groups were available (members of the *Charmus* group were not available for examination), in total 28 genera and 71 species. Including literature sources, we have confirmed these alignments in 68 genera (out of 82 total Recent genera defined in Buthoidea) spanning 407 species. For those cases where either the  $DM_c$  carina is vestigial, or, not illustrated in a particular figure, we made determination based on the relative position of  $d_3$  on the dorsal surface of the patella. In general, for members of the *Buthus* group, trichobothrium  $d_3$  is located roughly mid-segment from a vertical perspective, and, in members of the other groups,  $d_3$  is located lower on the segment. With respect to actual specimens we encountered no exceptions to the groupings defined above. Any presumed exceptions where found in literature illustrations only (these are discussed in the **Database** section). Also, in many genera, the  $DM_c$  carina was illustrated for some species and not for others. In these cases, the position of  $d_3$  on the patella was generally consistent.

We consider this character to be significant since it involves a trichobothrium “migrating” across a carina. Although one can detect some minor dislocations of individual trichobothria on the pedipalp surface, in general the overall topology of trichobothria distribution is quite constant thus providing excellent characters for the diagnoses of many taxonomic levels in scorpions. However, those minor dislocations never involve a trichobothrium moving across a carina, and therefore, we consider the latter to be a significant evolutionary event. There are several other important examples of this phenomenon in Recent scorpions: (1) the movement of chelal trichobothrium  $Et_2$  to the ventral surface in the bothriurids (superfamily Scorpionoidea), traversing the ventroexternal ( $VI$ ) carina; (2) chelal trichobothrium  $V_4$  dislocation to the external surface in many euscorpiids (superfamily Chactoidea), migrating across the  $VI$  carina; (3) chelal trichobothrium  $Eb_1$  moving to the ventral surface in many chactids (superfamily Chactoidea), again, crossing  $VI$ ; (4) patellar trichobothrium  $v_3$  moving to the external surface in the vaejovids (superfamily Chactoidea) and the iuroids (superfamily Iuroidea), traversing the  $VE_c$  carina; and (5) patellar trichobothrium  $v_2$  moving to the external surface in the typhlochactines (superfamily Chactoidea) across the  $VE_c$  carina. All of these examples are considered synapomorphies for these groups (Soleglad & Fet, 2003b).

**Alpha/beta pattern.** Vachon (1975) established the femoral *alpha/beta* trichobothrial pattern for the Type A configuration, specifically relevant to the buthoids. This somewhat simple observation on trichobothrial positions appears to be quite important in the high-level systematics of the Buthoidea. For example, Sissom (1990: 93) used this pattern as his primary couplet in his extensive key to buthoid genera (albeit, the key was not necessarily intended to be phylogenetic). Soleglad & Fet (2001) discussed this basic pattern as it related to the fossil scorpion *Archaeobuthus* and Recent scorpion *Pseudochactas*. These two species did not comply specifically with either *alpha* or *beta* patterns as originally defined by Vachon, although all five dorsal trichobothria present in these taxa were considered homologous to those found in Buthoidea (Soleglad & Fet, 2001). In their effort to determine the phylogenetic position of the primitive scorpion *Pseudochactas*, Soleglad & Fet (2003b) divided the original *alpha/beta* pattern into three subpatterns which would accommodate the patterns of both *Pseudochactas* and the fossil scorpion *Archaeobuthus*; the genus *Chaerilus* (superfamily Chaeroiloidea) was also considered. We adopt this refinement of the *alpha/beta* pattern as well in this paper [note: alignment with respect to the dorsoexternal carina is from a *midsegment* perspective]:

- *Alpha/beta* subpattern: alignment of  $d_1-d_3$ 
  - parallel to dorsoexternal carina (primitive)
  - points toward dorsoexternal carina ( $\beta$ )
  - points away from dorsoexternal carina ( $\alpha$ )
- *Alpha/beta* subpattern: alignment of  $d_3-d_4$ 
  - parallel to dorsoexternal carina (primitive)
  - points away from dorsoexternal carina ( $\beta$ )
  - points toward dorsoexternal carina ( $\alpha$ )
- *Alpha/beta* subpattern: placement of  $d_2$ 
  - on dorsal surface (primitive and  $\beta$ )
  - on internal surface ( $\alpha$ )

In Vachon's (1975: Figs.  $\alpha$ ,  $\beta$ ) original definition for the *alpha* pattern, trichobothria  $d_1-d_3$  point away from, and  $d_3-d_4$  point toward the dorsoexternal carina, and  $d_2$  is located on the internal surface. In contrast, these conditions are reversed in the *beta* pattern. In *Archaeobuthus*,  $d_1-d_3-d_4$  trichobothria are essentially in a straight line, thus both subpattern alignments are parallel to the dorsoexternal carina, and  $d_2$  is located on the dorsal surface, all of which Soleglad & Fet (2003b) hypothesized as primitive states. *Pseudochactas* exhibits the same pattern as *Archaeobuthus* except  $d_1-d_3$  points toward the dorsoexternal carina, which is a *beta* pattern characteristic. It was demonstrated by Soleglad & Fet (2003b: Fig. 115), using *Archaeobuthus* and *Pseudo-*

*chactas* as outgroups to the Buthoidea, that the *beta* pattern, in part, is primitive and the *alpha* pattern is a derivation from the *beta* pattern. In addition, also based on *Archaeobuthus* and *Pseudochactas*, Soleglad & Fet (2003b) considered the dorsal positioning of  $d_2$  to be primitive in the buthoids, and therefore, the internal position of  $d_2$  is derived.

In Figure 2 we illustrate the femoral trichobothrial pattern for *Archaeobuthus*, *Pseudochactas* and two versions each of the buthoid *alpha/beta* pattern. In Fig. 2 the *beta* pattern is divided into two subpatterns, the “pure” *beta*, where  $d_2$  is positioned dorsally, which is found in the *Buthus* and *Ananteris* groups (i.e., this pattern conforms to the original definition of Vachon, 1975); and the “diluted” *beta*, where  $d_2$  is positioned either on the dorsointernal carina or the internal surface of the femur, which is found in the *Isometrus* group. We have an analogous situation with the *alpha* pattern: the “pure” *alpha*, where  $d_2$  is positioned on the internal surface, found in the *Uroplectes* and *Tityus* groups (i.e., this pattern conforms to the original definition of Vachon, 1975); and the “diluted” *alpha*, where  $d_2$  exists on the dorsal surface, found in the *Charmus* group.

The determination of trichobothrial positions in the buthoids is a difficult task since, in general, individual trichobothria are somewhat smaller in size in this superfamily than in other Recent scorpions. Determining the position of trichobothrium  $d_2$  is even a more difficult task since it is petite in size. This is further complicated by the somewhat narrow tapering basal aspect of the pedipalp femur. In our examination of the literature illustrations we found only two genera where more than one species was depicted with trichobothrium  $d_2$  located on the dorsointernal carina, *Isometrus* and *Parabuthus*. In most of these cases, this was purely a judgment call since this carina is somewhat underdeveloped on the extreme basal portion of the segment. However, the stated difficulties aside, we do believe the distinctions described herein and illustrated in Fig. 2 are legitimate and provide additional information on the evolution of these five femoral trichobothria.

**Other observations of patellar trichobothria.** During the analysis of the  $d_3-DM_c$  alignment, we also conducted a preliminary analysis of the configuration of the seven external patellar trichobothria with respect to the exteromedian ( $EM_c$ ) carina. Based on literature only (in most part, specimens were not examined for this preliminary analysis) we concluded that trichobothria *est*, *esb*<sub>1</sub>, and *eb*<sub>1</sub> are located on the dorsal half of the segment whereas trichobothria *et*, *em*, *esb*<sub>2</sub>, and *eb*<sub>2</sub> are found on the ventral half of the segment, both sets of trichobothria being separated by the  $EM_c$  carina (consistent with Vachon's, 1974: Fig. 35, original depiction of the Type A pattern). We found no examples where a trichobothrium had migrated across this carina from either set, as is the case with trichobothrium  $d_3$  and  $DM_c$ .

However, we did detect an interesting configurational difference: in the *Tityus* group, and, in part, the *Uroplectes* group, the trichobothrial series  $esb_1$ – $esb_2$  are substantially separated from each other, the angle formed by  $esb_1$ – $esb_2$  angling considerably towards the distal aspect of the segment (i.e.,  $esb_2$  is positioned closer to trichobothrium *em* than is  $esb_1$ ); in contrast, in other groups of genera,  $esb_1$ – $esb_2$  are in close proximity, essentially parallel from a horizontal perspective (assuming the patella is positioned vertically). Genera complying to these two configurations of the  $esb_1$ – $esb_2$  series (based mostly on literature and some specimen examinations) are as follows:

**$esb_1$ – $esb_2$  in close proximity, essentially parallel.**  
***Buthus* group:** *Anomalobuthus*, *Buthacus*, *Buthoscorpio*, *Buthus*, *Compsobuthus*, *Hottentotta*, *Kraepelinia*, *Leiurus*, *Liobuthus*, *Mesobuthus*, *Microbuthus*, *Neobuthus*, *Paraorthochirus*, *Polisius*, *Razianus* and *Vachoniolus*. ***Ananteris* group:** *Ananteris* and *Lychas*; ***Isometrus* group:** *Isometrus* ( $esb_1$ – $esb_2$  exhibits some slight angling distally); ***Charmus* group:** *Charmus*, *Thaicharmus* (exhibits medium angling distally).

**$esb_1$ – $esb_2$  not in close proximity,  $esb_2$  positioned more distally.** *Uroplectes* group: *Butheoloides*, *Grosphus*, *Parabuthus* (in part), *Tityobuthus*, *Uroplectes*, and *Uroplectoides*; *Tityus* group: *Alayotityus* (slight angling) *Centruroides*, *Mesotityus*, *Microtityus*, *Ropalurus*, *Tityus*, and *Zabius* (as in *Alayotityus*, this genus  $esb_2$  is only slightly positioned above  $esb_1$ ; Luis Acosta, personal observation based on literature).

It must be stressed here that these observations are based on preliminary data only. In addition, it is important to note that minor localized dislocation of patellar trichobothria, especially in a vertical direction, is somewhat common in scorpions (whereas migration of a trichobothrium across a carina is not). Therefore, this data must be solidified with more genera and species in order to ascertain if these two *esb* configurations are important in any major phylogenetic sense. It does seem clear, however, based on this preliminary analysis alone, that it probably is valid for the New World *Tityus* group, where the pattern is the most exaggerated, and possibly for the Old World *Uroplectes* group as well. If this holds true, then we have another synapomorphy for the clade (*Uroplectes* group + *Tityus* group), both of these groups exclusively exhibiting a “pure” form of the *alpha* pattern.

**Tibial spurs.** The tibial spur is considered an important character in scorpion systematics. In particular it has been considered a major character in buthoid taxonomy. Sissom (1990: 93–100) used the presence/absence

of this spur as a second-level couplet in no less than three places in his key to buthoid genera. Although the tibial spur is present in many fossil scorpions—e.g., *Compsoscorpius* (Jeram, 1994a: Text-Fig. 5-D), *Palaeburmesebuthus* (Santiago-Blay et al. 2004a), *Pulmonoscorpius* (Jeram, 1994b)—there is a great variability in Recent scorpions. In the primitive parvorders, the tibial spurs are present on legs III–IV in Pseudochactida (presumably plesiomorphic), absent in Chaerilida, and variable in Buthida. In Buthida, tibial spurs are absent in New World genera, and variable within the Old World members, although showing consistency across many genera. We consider the consistent loss of the tibial spur in the New World buthids, all exclusively members of the *Tityus* group, an important derivation. We do not, however, consider the scattered loss of the tibial spurs in the Old World buthoids necessarily important phylogenetically. Table 1 shows that tibial spur loss occurs in three Old World groups, the *Buthus*, *Ananteris*, and *Isometrus* groups. Furthermore, in certain Old World psammophilic genera (e.g., *Anomalobuthus*, *Aristobuthus*, *Liobuthus*, *Pectinibuthus*, *Plesiobuthus*, *Sabinebuthus*, *Vachoniolus*, etc.) we see either a reduction or the complete absence of these spurs, presumably a factor of microhabitat adaptation (Fet et al., 1998). The independent DNA-based phylogeny of Fet et al. (2003) for 17 genera of Buthidae demonstrated the polyphyletic origin of psammophily among these genera; the full or partial tibial spur loss is observed independently in at least three lineages including psammophilic genera *Anomalobuthus*, *Liobuthus*, and (*Vachoniolus* + *Aristobuthus*). In addition, as reported by Soleglad & Fet (2003b), the tibial spur appears to be a vestigial structure in Recent scorpions, since it exhibits little or no structure within the membrane from which it extends (personal observation of Graeme Lowe on *Aristobuthus*). This observation, of course, is based only on a single species, but one might assume, if it holds true for the superfamily in general, that due to its vestigial nature it is highly susceptible to loss or near loss due to microhabitat pressures. Finally, we might add that the tibial spur exhibited in fossil scorpions probably was not vestigial, perhaps performing some adaptive function.

## Database

The list below includes 82 currently valid genera of Buthoidea (Soleglad et al., 2005, with additions from Lourenço, 2000g, 2003a, 2004a) partitioned in the hypothesized groups. For each genus, we partition the data into groups where the  $DM_c$  carina is visible and where it is not. For the genera marked with an asterisk (\*), the position of  $d_3$  with respect to  $DM_c$  has still to be verified since no drawings of dorsal patella were available in literature. The number of species evaluated per genus is stated. In addition, we characterize six known fossil

genera of Buthidae. For those few examples where apparent exceptions to the two patellar trichobothria alignments occur, they are noted as such. These exceptions are discussed individually at the end of this section.

Note: for the genera whose  $d_3$ – $DM_c$  alignment is not known, we tentatively stipulate their group association based on close affinity to other genera, geographic locality, and/or other characters. Clearly, the alignment for these genera must be determined before final group placement can be established.

Since in a large majority of cases presented below the data are consistent within a genus, we consider these data as an empirical “proof” of the legitimacy of the new character described in this paper.

#### **Patellar trichobothrium $d_3$ internal to carina $DM_c$**

**“Buthus group”.** Trichobothrial pattern *beta*, femur trichobothrium  $d_2$  located dorsally (39 genera); tibial spur is lost in *Lanzatus*, *Liobuthus*, *Pectinibuthus*, *Plesiobuthus*, *Sabinebuthus*, and *Vachoniolus*.

***Androctonus*** Ehrenberg, 1828 (12 species):  **$DM_c$  visible:** *A. amoreuxi* (Audouin, 1826) (Vachon, 1952: Fig. 218; Vachon, 1958: Fig. 2); *A. amoreuxi levyi* Fet, 1997 (Levy & Amitai, 1980: Fig. 45, as *A. a. hebraeus*); *A. australis* (Linnaeus, 1758) (Vachon, 1952: Fig. 203; Levy & Amitai, 1980: Fig. 41); *A. baluchicus* Pocock, 1900 (Lourenço, 2005b: Fig. 15); *A. bicolor* Ehrenberg, 1828 (Fig. 4, specimen examined; Vachon, 1952: Figs. 159, 166, as *A. aeneas*; Levy & Amitai, 1980: Fig. 37, as *A. b. bicolor*; Lourenço, 2005b: Fig. 34); *A. crassicauda* (Olivier, 1807) (Vachon, 1952: Fig. 172; Levy & Amitai, 1980: Fig. 33; specimen examined); *A. dekeyseri* Lourenço, 2005 (Lourenço, 2005b: Fig. 29); *A. gonneti* Vachon, 1948 (Lourenço, 2005b: Fig. 9); *A. hoggarensis* (Pallary, 1929) (Vachon, 1952: Fig. 194; Lourenço, 2005b: Fig. 45); *A. liouvillei* (Pallary, 1924) (Lourenço, 2005b: Fig. 37); *A. maelfaiti* Lourenço, 2005 (Lourenço, 2005b: Fig. 21); *A. mauritanicus* (Pocock, 1902) (Vachon, 1952: Fig. 177; Lourenço, 2005b: Fig. 41); *A. sergenti* Vachon, 1948 (Vachon, 1952: Fig. 191; Lourenço, 2005b: Fig. 47).

***Anomalobuthus*** Kraepelin, 1900 (one species):  **$DM_c$  visible:** *A. rickmersi* Kraepelin, 1900 (Fig. 10, specimen examined).

***Aristobuthus*** Finnegan, 1932 (one species):  **$DM_c$  visible:** *A. pterygocerus* Finnegan, 1932 (Vachon, 1960a: Fig. 2; Lourenço, 1998b: Fig. 4; specimen examined).

\****Baloorthochirus*** Kovařík, 1996 (=*Pakistanorthochirus* Lourenço, 1997) (placed here since the genus is close to *Orthochirus*; see Kovařík, 1996, 2004).

***Birulatus*** Vachon, 1974 (one species):  **$DM_c$  visible:** *B. astartiae* Stathi et Lourenço, 2003 (Stathi & Lourenço, 2003: Fig. 8).

***Buthacus*** Birula, 1908 (ten species):  **$DM_c$  visible:** *B. elevai* Lourenço, 2001 (Lourenço, 2001c: Fig. 21); *B. mahraoui* Lourenço, 2004 (Lourenço, 2004g: Fig. 8); *B. villiersi* Vachon, 1949 (Vachon, 1952: Fig. 248); *B. yotvatensis* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 33; Fig. 11; Levy & Amitai, 1980: Fig. 84; Fig. 11,  $DM_c$  visible as smooth carina in specimen examined).  **$DM_c$  not visible:** *B. arenicola* (Simon, 1885) (Vachon, 1952: Fig. 256; Levy & Amitai, 1980: Fig. 80); *B. foleyi* Vachon, 1948 (Vachon, 1952: Fig. 236); *B. huberi* Lourenço, 2001 (Lourenço, 2001c: Fig. 8); *B. leptochelys* (Ehrenberg, 1829) (Vachon, 1952: Fig. 263; Levy & Amitai, 1980: Fig. 73; Lourenço, 2004c: Fig. 13); *B. leptochelys nitzani* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 22; Levy & Amitai, 1980: Fig. 77); *B. yotvatensis nigroaculeatus* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 39); *B. striffleri* Lourenço, 2004 (Lourenço, 2004c: Fig. 4); *B. ziegleri* Lourenço, 2000 (Lourenço, 2000c: Fig. 6), **exception**,  $d_3$  external to  $DM_c$ .

***Butheolus*** Simon, 1882 (three species):  **$DM_c$  visible:** *B. gallagheri* Vachon, 1980 (specimen examined); *B. thalassinus* Simon, 1882 (Sissom, 1994: Fig. 11; specimen examined).  **$DM_c$  not visible:** *B. anthracinus* (Pocock, 1897) (specimen examined).

***Buthiscus*** Birula, 1905 (one species):  **$DM_c$  visible:** *B. bicalcaratus* Birula, 1905 (Vachon, 1952: Fig. 113; Lourenço, 2002b: Fig. 5).

***Buthus*** Leach, 1815 (eight species):  **$DM_c$  visible:** *B. atlantis* Pocock, 1889 (Vachon, 1952: Fig. 356); *B. bonito* Lourenço et Geniez, 2005 (Lourenço & Geniez, 2005: Fig. 6); *B. draa* Lourenço et Slimani, 2004 (Lourenço & Slimani, 2004: Figs. 3, 6); *B. ibericus* Lourenço et Vachon, 2004 (Lourenço & Vachon, 2004: Fig. 36); *B. jianxinae* Lourenço, 2005 (Lourenço, 2005a: Fig. 3); *B. maroccanus* Birula, 1903 (Vachon, 1952: Fig. 369); *B. montanus* Lourenço et Vachon, 2004 (Lourenço & Vachon, 2004: Fig. 26); *B. occitanus* (Amoreux, 1789) (Vachon, 1952: Figs. 342, 389, 390, 404, 413, 424, 429, 441, 446; Lourenço & Vachon, 2004: Fig. 8; specimen examined); *B. occitanus israelis* (Shulov et Amitai, 1959) (Levy & Amitai, 1980: Fig. 28).

***Cicileus*** Vachon, 1948 (two species):  **$DM_c$  visible:** *C. cloudsleythompsoni* Lourenço, 1999 (Lourenço, 1999d: Fig. 6); *C. exilis* (Pallary, 1928) (Vachon, 1952: Fig. 96).

***Compsobuthus*** Vachon, 1949 (17 species):  **$DM_c$  visible:** *C. acutecarinatus* (Simon, 1882) (Vachon, 1940a:

Fig. 9, as *Buthus*; Sissom, 1994: Fig. 16; specimen examined); *C. andresi* Lourenço, 2004 (Lourenço, 2004d: Fig. 5); *C. arabicus* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 18); *C. brevimanus* (Werner, 1936) (Sissom, 1994: Fig. 22; specimen examined); *C. carmelitus* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 2; Levy & Amitai, 1980: Fig. 66); *C. garyi* Lourenço et Vachon, 2001 (Lourenço & Vachon, 2001: Fig. 8); *C. jordanensis* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 12); *C. longipalpis* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 8; Levy & Amitai, 1980: Fig. 69); *C. maindroni* (Kraepelin, 1900) (specimen examined); *C. matthiesseni* (Birula, 1905) (Sissom & Fet, 1998: Fig. 5; Fig. 9, specimen examined); *C. polisi* Lowe, 2001 (Lowe, 2001: Fig. 7); *C. rugosulus* (Pocock, 1900) (Lourenço & Monod, 1998: Fig. 5; specimen examined); *C. simoni* Lourenço, 1999 (Lourenço, 1999e: Fig. 14); *C. tofti* Lourenço, 2001 (Lourenço, 2001d: Fig. 6); *C. vachoni* Sissom, 1994 (Sissom, 1994: Fig. 35); *C. werneri* (Birula, 1908) (Vachon, 1952: Fig. 289; Levy & Amitai, 1980: Fig. 60; Sissom, 1994: Fig. 29 specimen examined); *C. werneri schmiedeknechti* Vachon, 1949 (Levy & Amitai, 1980: Fig. 60, as *C. w. judaicus*); *C. williamsi* Lourenço, 1999 (Lourenço, 1999e: Fig. 8).

***Congobuthus*** Lourenço, 1999 (one species): ***DM<sub>c</sub>* visible:** *C. fagei* Lourenço, 1999 (Lourenço, 1999c: Fig. 12)

\****Darchenia*** Vachon, 1977 (placed here since the genus is close to *Compsobuthus*; see Lourenço, 1995).

***Hemibuthus*** Pocock, 1900 (one species): ***DM<sub>c</sub>* visible:** *H. crassimanus* Pocock, 1900 (Vachon, 1960b: Fig. 2; Tikader & Bastawade, 1983: Fig. 297).

***Hottentotta*** Birula, 1908 (12 species): ***DM<sub>c</sub>* visible:** *H. acostai* Lourenço, 2004 (Lourenço, 2004b: Fig. 6); *H. alticola kabulensis* Vachon, 1958 (Vachon, 1958: Fig. 14, as *Buthotus*); *H. arenaceus* (Purcell, 1901) (Lamoral, 1979: Fig. 48, as *Buthotus*); *H. conspersus* (Thorell, 1877) (Lamoral, 1979: Fig. 69, as *Buthotus*); *H. franzwerneri* (Birula, 1914) (Vachon, 1952: Fig. 326, as *Buthotus*); *H. hottentotta* (Fabricius, 1787) (Vachon, 1940a: Fig. 3, as *Buthus*; specimen examined); *H. minax* (L. Koch, 1875) (specimen examined); *H. judaicus* (Simon, 1872) (Vachon, 1952: Fig. 319, as *Buthotus*; Levy & Amitai, 1980: Fig. 55, as *Buthotus*; specimen examined); *H. socotrensis* (Pocock, 1889) (Vachon, 1979: Fig. 3, as *Buthotus*); *H. trilineatus* (Peters, 1861) (specimen examined). ***DM<sub>c</sub>* not visible:** *H. geffardi* Lourenço, 2000 (Lourenço, 2000b: Fig. 2); *H. jayakari* (Pocock, 1895) (specimen examined).

***Iranobuthus*** Kovařík, 1997 (one species): ***DM<sub>c</sub>* visible:** *I. krali* Kovařík, 1997 (Kovařík, 1997b: Fig. 10).

***Kraepelinia*** Vachon, 1974 (one species): ***DM<sub>c</sub>* visible:** *K. palpator* (Birula, 1903) (Vachon, 1974: 236; specimen examined)

***Lanzatus*** Kovařík, 2001 (one species): ***DM<sub>c</sub>* not visible:** *L. somalicus* Kovařík, 2001 (Kovařík, 2001: Fig. 5).

***Leiurus*** Ehrenberg, 1828 (two species): ***DM<sub>c</sub>* visible:** *L. jordanensis* Lourenço, Modry et Amr, 2002 (Lourenço et al., 2002: Fig. 5); *L. quinquestriatus* (Ehrenberg, 1828) (Vachon, 1952: Fig. 275; Sissom, 1994: Fig. 41; specimen examined); *L. quinquestriatus hebraeus* (Birula, 1908) (Levy & Amitai, 1980: Fig. 50).

***Liobuthus*** Birula, 1898 (one species): ***DM<sub>c</sub>* visible:** *L. kessleri* Birula, 1898 (Fig. 7, specimen examined).

***Lissothus*** Vachon, 1948 (one species): ***DM<sub>c</sub>* not visible:** *L. bernardi* Vachon, 1944 (Vachon, 1952: Fig. 126); **femur trichobothrium d<sub>2</sub> absent** (placed here tentatively due to general morphology and biogeographic connections).

***Mesobuthus*** Vachon, 1950 (eight species): ***DM<sub>c</sub>* visible:** *M. caucasicus* (Nordmann, 1840) (Fig. 6, specimen examined); *M. caucasicus parthorum* (Pocock, 1900) (Vachon, 1958: Fig. 33); *M. eupeus haarlovi* Vachon, 1958 (Vachon, 1958: Fig. 43); *M. martenii* (Karsch, 1879) (Qi et al., 2004: Fig. 12); *M. songi* Lourenço, Qi et Zhu, 2005 (Lourenço et al., 2005b: Fig. 13); *M. tamulus gangeticus* (Pocock, 1900) (Tikader & Bastawade, 1983: Fig. 597); *M. tamulus gujaratensis* (Pocock, 1900) (Tikader & Bastawade, 1983: Fig. 572). ***DM<sub>c</sub>* not visible:** *M. hendersoni* (Pocock, 1900) (Tikader & Bastawade, 1983: Fig. 647); *M. pachyurus* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 698); *M. rugiscutis* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 672); *M. tamulus* (Fabricius, 1798) (Vachon, 1940b: Fig. 15, as *Buthus grammurus*; Tikader & Bastawade, 1983: Fig. 621); *M. tamulus concanensis* (Pocock, 1900) (Tikader & Bastawade, 1983: Fig. 523); *M. tamulus sindicus* (Pocock, 1900) (Tikader & Bastawade, 1983: Fig. 547).

***Microbuthus*** Kraepelin, 1898; **femur trichobothrium d<sub>2</sub> absent** (three species): ***DM<sub>c</sub>* visible:** *M. fagei* Vachon, 1949 (Vachon, 1952: Fig. 470); *M. fagei marocannus* Lourenço, 2002 (Lourenço, 2002a: Fig. 16); *M. pusillus* Kraepelin, 1898 (Vachon, 1952: Fig. 471; Lourenço, 2002a: Fig. 12); *M. sp.* (Fig. 12, specimen examined).

***Neobuthus*** Hirst, 1911 (two species): ***DM<sub>c</sub>* not visible:** *N. cloudsleythompsoni* Lourenço, 2001 (Lourenço, 2001h: Fig. 17); *N. sudanensis* Lourenço, 2005 (Lourenço, 2005a: Fig. 24).

***Odontobuthus*** Vachon, 1950 (three species): ***DM<sub>c</sub>* visible:** *O. bidentatus* Lourenço et Pézier, 2002 (Lourenço & Pézier, 2002a: Fig. 26); *O. doriae* (Thorell, 1877) (specimen examined). ***DM<sub>c</sub>* not visible:** *O. odonturus* (Pocock, 1897) (specimen examined).

***Orthochiroides*** Kovařík, 1998 (one species):  **$DM_c$  visible:** *O. vachoni* Kovařík, 1998 (Kovařík, 1998: Fig. 17).

***Orthochirus*** Karsch, 1891 (seven species):  **$DM_c$  visible:** *O. afghanus* Kovařík, 2004 (Kovařík, 2004: Fig. 3;  $DM_c$  not shown?); *O. bicolor* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 346); *O. flavescentis* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 314); *O. innesi* Simon, 1910 (Vachon, 1952: Fig. 306); *O. krischnai* (Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 362); *O. pallidus* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 330); *O. scrobiculosus negebensis* (Shulov et Amitai, 1960) (Fig. 8, specimen examined; Levy & Amitai, 1980: Fig. 89).

***Paraorthochirus*** Lourenço & Vachon, 1997 (four species):  **$DM_c$  visible:** *P. glabrifrons* (Kraepelin, 1903) (type specimen examined); *P. goyffoni* Lourenço et Vachon, 1995 (Lourenço & Vachon, 1995: Fig. 15); *P. kinzelbachi* Lourenço et Huber, 2000 (Lourenço & Huber, 2000: Fig. 7); *P. stockwelli* Lourenço et Vachon, 1995 (Lourenço & Vachon, 1995: Fig. 9).

***Pectinibuthus*** Fet, 1984 (one species):  **$DM_c$  not visible:** *P. birulai* Fet, 1984 (Fet, 1987: Fig. 4).

***Plesiobuthus*** Pocock, 1900 (one species):  **$DM_c$  visible:** *P. paradoxus* Pocock, 1900 (Capes & Fet, 2001: Fig. 3).

***Polisius*** Fet, Capes et Sissom, 2001 (one species):  **$DM_c$  visible:** *P. persicus* Fet, Capes et Sissom, 2001 (Fet et al., 2001: Fig. 4).

\****Psammobuthus*** Birula, 1911 (this genus is a possible synonym of *Anomalobuthus*; A. Gromov, pers. comm., 2002).

***Razianus*** Farzanpay, 1987 (=*Neohemibuthus* Lourenço, 1996) (one species):  **$DM_c$  visible:** *R. zarudnyi* (Birula, 1903) (Fig. 5, specimen examined; Lourenço, 1996d: Fig. 6, as *Neohemibuthus kinzelbachi*).

\****Sabinebuthus*** Lourenço, 2001 (placed here since the genus is close to *Anomalobuthus*; see Lourenço, 2001a).

\****Sassanidothus*** Farzanpay, 1987 (placed here since the genus is close to *Mesobuthus*; see Vachon, 1958)

\****Simonoides*** Vachon et Farzanpay, 1987 (placed here since the genus is close to *Orthochirus*).

\****Somalibuthus*** Kovařík, 1998 (placed here tentatively based on general morphology; see Kovařík, 1998).

***Vachoniolus*** Levy, Amitai et Shulov, 1973 (two species):  **$DM_c$  not visible:** *V. globimanus* Levy, Amitai et Shulov, 1973 (Levy et al., 1973: Fig. 43); *V. minipectenibus* (Levy, Amitai et Shulov, 1973) (Levy et al., 1973: Fig. 28, as *Buthacus*).

***Vachonus*** Tikader et Bastawade, 1983 (two species):  **$DM_c$  visible:** *V. atrostriatus* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 501); *V. rajasthanicus* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 488).

**Patellar trichobothrium  $d_3$  external to carina  $DM_c$**

“***Ananteris* group**”. Trichobothrial pattern ***beta***; femur trichobothrium  $d_2$  located dorsally: (6 genera); tibial spur is lost in *Akentrobuthus*.

***Akentrobuthus*** Lamoral, 1976 (one species):  **$DM_c$  visible:** *A. leleupi* Lamoral, 1976 (Lamoral, 1976: Fig. 5).

***Ananteris*** Thorell, 1891 (21 species):  **$DM_c$  visible:** *A. asmolei* Lourenço, 1981 (Lourenço, 1981: Fig. 24); *A. dekeyseri* Lourenço, 1982 (Lourenço, 1982b: Fig. 74); *A. evelynae* Lourenço, 2004 (Lourenço, 2004f: Fig. 3).  **$DM_c$  not visible:** *A. balzani* Thorell, 1891 (Lourenço, 1982b: Fig. 8; Lourenço, 2001g: Fig. 10); *A. charlescorfieldi* Lourenço, 2001 (Lourenço, 2001g: Fig. 8); *A. coineau* Lourenço, 1982 (Lourenço, 1982b: Fig. 76); *A. cussini* Borelli, 1910 (González-Sponga, 1996b: Fig. 276; Lourenço & Huber, 1999a: Fig. 4); *A. elisabethae* Lourenço, 2003 (Lourenço, 2003d: Fig. 19); *A. feae* (Borelli, 1911) (Lourenço, 1985: Fig. 16); *A. festae* Borelli, 1899 (Lourenço, 1982b: Fig. 78; Lourenço, 1999e: Fig. 8); *A. francke* Lourenço, 1982 (Lourenço, 1982b: Fig. 72); *A. leilae* Lourenço, 1999 (Lourenço, 1999e: Fig. 4); *A. luciae* Lourenço, 1984 (Lourenço, 1984c: Fig. 4); *A. mariaelenae* Lourenço, 1999 (Lourenço, 1999f: Fig. 2); *A. mariaterzae* Lourenço, 1982 (Lourenço, 1982b: Fig. 71); *A. mauryi* Lourenço, 1982 (Lourenço, 1982b: Fig. 73); *A. nairae* Lourenço, 2004 (Lourenço, 2004e: Fig. 8); *A. pydanieli* Lourenço, 1982 (Lourenço, 1982b: Fig. 75); *A. sabineae* Lourenço, 2001 (Lourenço, 2001g: Fig. 2F); *A. turumbanensis* González-Sponga, 1980 (González-Sponga, 1996b: Fig. 282); *A. venezuelensis* González-Sponga, 1982 (Lourenço, 1982b: Fig. 77; González-Sponga, 1996b: Fig. 279).

***Himalayotityobuthus*** Lourenço, 1997 (one species):  **$DM_c$  visible:** *H. alejandraise* Lourenço, 2003 (Lourenço, 2003b: Fig. 12).

***Lychas*** C. L. Koch, 1845 (14 species):  **$DM_c$  visible:** *L. albimanus* Henderson, 1919 (Tikader & Bastawade, 1983: Fig. 251); *L. biharensis* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 267); *L. ceylonensis* Lourenço et Huber, 1999 (Lourenço & Huber, 1999b: Fig. 3); *L. flavimanus* (Thorell, 1888) (Vachon, 1986: Fig. 17); *L. hender-*soni (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 180); *L. laevifrons* Pocock, 1897 (Tikader & Bastawade, 1983: Fig. 213); *L. mucronatus* (Fabricius, 1798) (Tikader & Bastawade, 1983: Fig. 150: exception,  $d_3$  internal to  $DM_c$ ); *L. nigristernis* (Pocock, 1899) (Tikader & Bastawade, 1983: Fig. 111);

*L. rugosus* (Pocock, 1897) (Tikader & Bastawade, 1983: Fig. 166: **exception**,  $d_3$  internal to  $DM_c$ ); *L. scaber* (Pocock, 1893) (Tikader & Bastawade, 1983, Fig. 235: **exception**,  $d_3$  above  $DM_c$ ); *L. sri-lankensis* Lourenço, 1997 (Lourenço, 1997f: Fig. 4; **exception**,  $d_3$  internal to  $DM_c$ ); *L. tricarinatus* (Simon, 1884) (Tikader & Bastawade, 1983: Fig. 197); *L.* sp. (Fig. 13, specimen examined, Singapore); *L.* sp. (specimen examined, Indonesia).  **$DM_c$  not visible:** *L. gravelyi* Henderson, 1913 (Tikader & Bastawade, 1983: Fig. 126); *L. kamshetensis* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 282).

\****Lychasoides*** Vachon, 1974 (one species): *L. amieti* Vachon, 1974 (placed here since the genus is close to *Ananteris*; Lourenço, 1999j).

\****Microananteris*** Lourenço, 2003 (one species):  **$DM_c$  not visible:** *M. minor* Lourenço, 2003 (placed here since the genus is close to *Ananteris*; Lourenço, 2003a).

**“Isometrus group”.** Trichobothrial pattern *beta*; femur trichobothrium  $d_2$  located internally, or on internal carina or absent (7 genera); tibial spur is lost in *Afroisometrus* and *Isometrus*

\****Afroisometrus*** Kovařík, 1997 (one species): *A. minishullae* (FitzPatrick, 1994) (Kovařík, 1997) (placement according to phylogeny of Prendini, 2004b).

***Australobuthus*** Locket, 1990 (one species):  **$DM_c$  visible:** *A. xerolimniorum* Locket, 1990 (Locket, 1990: Figs. 10B, 11A).

***Babycurus*** Karsch, 1886 (six species):  **$DM_c$  visible:** *B. exquisitus* Lowe, 2000 (Lowe, 2000: Fig. 7); *B. jacksoni* (Pocock, 1890) (Vachon, 1940b: Fig. 14); *B. kirki* Pocock, 1890 (Vachon, 1940a: Fig. 13, as *Buthus*); *B. melanicus* Kovařík, 2000 (Prendini, 2004a: Fig. 7); *B. solegladi* Lourenço, 2005 (Lourenço, 2005a: Fig. 15); *B. zambonellii* Borelli, 1902 (Sissom, 1994: Fig. 4).

***Hemilychas*** Hirst, 1911 (one species):  **$DM_c$  visible:** *H. alexandrinus* Hirst, 1911 (Locket, 1990: Fig. 11B, as *Lychas*; see also Kovařík, 1997a).

***Isometroides*** Keyserling, 1885 (one species):  **$DM_c$  visible:** *I. vescus* (Karsch, 1880) (Locket, 1990: Fig. 11C; Lourenço, 2003b: Fig. 4; specimen examined).

***Isometrus*** Ehrenberg, 1828 (18 species):  **$DM_c$  visible:** *I. acanthurus* Pocock, 1899 (Tikader & Bastawade, 1983: Fig. 877); *I. acanthurus loebli* Vachon, 1982 (Vachon, 1982: Fig. 60); *I. assamensis* Oates, 1888 (Tikader & Bastawade, 1983: Fig. 862); *I. basilicus* Karsch, 1879 (Vachon, 1982: Fig. 42); *I. besucheti* Vachon, 1982 (Vachon, 1982: Fig. 53); *I. brachycentrus* Pocock, 1899 (Tikader & Bastawade, 1983: Fig. 766); *I. corbetti* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 893); *I. hain-*

*anensis* Lourenço, Qi et Zhu, 2005 (Lourenço et al., 2005a: Fig. 5); *I. heimi* Vachon, 1976 (Vachon, 1976: Fig. 5); *I. isadensis* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 809); *I. kurkai* Kovařík, 1997 (Kovařík, 1997d: Fig. 4); *I. maculatus* (DeGeer, 1778) (Vachon, 1972: Figs. 3, 11; Tikader & Bastawade, 1983: Fig. 836, as *I. europaeus*; González-Sponga, 1996b: Fig. 295; Fig. 14, specimen examined); *Isometrus melanodactylus* (L. Koch, 1867) (specimen examined); *I. rigidulus* Pocock, 1897 (Tikader & Bastawade, 1983: Fig. 752); *I. thurstoni* Pocock, 1893 (Tikader & Bastawade, 1983: Fig. 794); *I. thwaitesi* Pocock, 1897 (Vachon, 1982: Fig. 30); *I. thwaitesi pallidus* Lourenço et Huber, 2002 (Lourenço & Huber, 2002: Fig. 4); *I. vittatus* Pocock, 1900 (Tikader & Bastawade, 1983: Fig. 736; **exception**,  $d_3$  internal to  $DM_c$ ); *I. zideki* Kovařík, 1994 (Kovařík, 1994: Fig. 3).  **$DM_c$  not visible:** *I. sankeriensis* Tikader et Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 907).

\****Odonturus*** Karsch, 1879 (one species): *O. dentatus* Karsch, 1879 (placement according to phylogeny of Prendini, 2004b).

**“Charmus group”.** Trichobothrial pattern *alpha*; femur trichobothrium  $d_2$  located dorsally (3 genera); tibial spurs present.

***Charmus*** Karsch, 1879 (five species):  **$DM_c$  not visible:** *C. brignolii* Lourenço, 2000 (Lourenço, 2000e: Fig. 13); *C. indicus* Hirst, 1915 (Lourenço, 2000e: Fig. 7; Tikader & Bastawade, 1983: Fig. 392); *C. laneus* Karsch, 1879 (Vachon, 1982: Fig. 4); *C. minor* Lourenço, 2002 (Lourenço, 2002c: Fig. 13, 14); *C. sinhagadensis* Tikader & Bastawade, 1983 (Tikader & Bastawade, 1983: Fig. 412).

***Somalicharmus*** Kovařík, 1998 (one species):  **$DM_c$  not visible:** *S. whitmanae* Kovařík, 1998 (Kovařík, 1998: Fig. 12).

***Thaicharmus*** Kovařík, 1995 (one species):  **$DM_c$  not visible:** *T. mahunkai* Kovařík, 1995 (Kovařík, 1995: Fig. 10).

**“Uroplectes group”.** Trichobothrial pattern *alpha*; femur trichobothrium  $d_2$  located internally or absent; (18 genera); tibial spurs present (Old World, including all three genera of Microcharmidæ)

***Ankaranocharmus*** Lourenço, 2004 (one species):  **$DM_c$  not visible:** *A. pauliani* Lourenço, 2004 (Lourenço, 2004a: Fig. 19) (currently under Microcharmidæ); **femur trichobothrium  $d_2$  absent** (placed here tentatively due to general morphology and biogeographic connections).

***Butheoloides*** Hirst, 1925 (nine species): ***DM<sub>c</sub>* visible:** *B.* (*Gigantoloides*) *aymerichi* Lourenço, 2002 (Lourenço, 2002e: Fig. 6), **exception,** *d<sub>3</sub>* internal to *DM<sub>c</sub>*. ***DM<sub>c</sub>* not visible:** *B. annieae* Lourenço, 1986 (Lourenço, 1986a: Fig. 16); *B. charlotteae* Lourenço, 2000 (Lourenço, 2000f: Fig. 5); *B. hirsti* Lourenço, 1996 (Lourenço, 1996b: Fig. 17); *B. maroccanus* Hirst, 1925 (Vachon, 1952: Fig. 129); *B. monodi* Vachon, 1950 (Vachon, 1950a: Fig. 2); *B. occidentalis* Lourenço, Slimani et Berahou, 2003 (Lourenço et al., 2003: Fig. 15); *B. polisi* Lourenço, 1996 (Lourenço, 1996b: Fig. 12); *B. schwendingeri* Lourenço, 2002 (Lourenço, 2002e: Fig. 8); *B. wilsoni* Lourenço, 1995 (Lourenço, 1995a: Fig. 4).

***Buthoscorpio*** Werner, 1936 (two species): ***DM<sub>c</sub>* not visible:** *B. politus* (Pocock, 1899) (Vachon, 1961: Fig. 1; Tikader & Bastawade, 1983: Fig. 427, as *Stenochirus*); *B. sarasinorum* (Karsch, 1891) (Vachon, 1982: Fig. 14, as *Stenochirus*; Tikader & Bastawade, 1983: Fig. 449, as *Stenochirus*).

\****Egyptobuthus*** Lourenço, 1999 (placed here since the genus is close to *Butheoloides*; Lourenço, 1999k).

***Grosphus*** Simon, 1880 (12 species): ***DM<sub>c</sub>* not visible:** *G. ankafantsika* Lourenço, 2003 (Lourenço, 2003f: Fig. 14); *G. ankarana* Lourenço & Goodman, 2003 (Lourenço & Goodman, 2003b: Fig. 21); *G. darainensis* Lourenço, Goodman et Ramilijaona (Lourenço et al., 2004b: Fig. 7); *G. flavopiceus* Kraepelin, 1900 (Lourenço & Goodman, 2003b: Fig. 29); *G. garciai* Lourenço, 2001 (Lourenço, 2001j: Fig. 9); *G. griveaudi* Vachon, 1969 (Vachon, 1969: Fig. 2); *G. hirtus* Kraepelin, 1901 (Fig. 15, specimen examined); *G. intertidialis* Lourenço, 1999 (Lourenço, 1999h: Fig. 2); *G. madagascariensis* (Gervais, 1843) (specimen examined); *G. mahafaliensis* Lourenço, Goodman et Ramilijaona (Lourenço et al., 2004b: Fig. 3); *G. olgae* Lourenço, 2004 (Lourenço, 2004i: Fig. 3); *G. simoni* Lourenço, Goodman et Ramilijaona (Lourenço et al., 2004b: Fig. 11).

***Karasbergia*** Hewitt, 1913 (one species): ***DM<sub>c</sub>* visible:** *K. methueni* Hewitt, 1913 (Lamoral, 1979: Fig. 78); **femur trichobothrium *d<sub>2</sub>* absent.**

***Microcharmus*** Lourenço, 1996 (one species): ***DM<sub>c</sub>* visible:** *M. hauseri* Lourenço, 1996 (Lourenço, 1996c: Fig. 18, specimen examined, male holotype) (currently under Microcharmidae).

***Neogrosphus*** Lourenço, 1995 (one species): ***DM<sub>c</sub>* not visible:** *N. blinci* Lourenço, 1996 (Lourenço, 1996a: Fig. 23).

***Neoprotobuthus*** Lourenço, 2000 (one species): *DM<sub>c</sub>* not visible: *N. intermedius* Lourenço, 2000 (Lourenço, 2000a: Fig. 3) (currently under Microcharmidae).

\****Palaeogrosphus*** Lourenço, 2000 (placed here since the genus is close to *Grosphus*; Lourenço, 2000g).

***Parabuthus*** Pocock, 1890 (17 species): ***DM<sub>c</sub>* visible:** *P. gracilis* Lamoral, 1979 (Lamoral, 1979: Fig. 114); *P. granulatus* (Ehrenberg, 1828) (Lamoral, 1979: Fig. 121; specimen examined); *P. kraepelini* (Werner, 1902) (Lamoral, 1979: Fig. 137); *P. muelieri* Prendini, 2000 (Prendini, 2000: Fig. 4; Prendini, 2003: Fig. 10); *P. namibensis* Lamoral, 1979 (Lamoral, 1979: Fig. 161); *P. schlechteri* Purcell, 1899 (Lamoral, 1979: Fig. 185); *P. stridulus* Hewitt, 1913 (Lamoral, 1979: Fig. 195); *P. sp.* (Fig. 16, specimen examined). ***DM<sub>c</sub>* not visible:** *P. brevimanus* (Thorell, 1877) (Lamoral, 1979: Fig. 91); *P. kalaharicus* Lamoral, 1977 (Lamoral, 1979: Fig. 130); *P. kraepelini* Werner, 1902 (Lamoral, 1979: Fig. 137); *P. kuanyamarum* Monard, 1937 (Lamoral, 1979: Fig. 145); *P. laevifrons* (Simon, 1887) (Lamoral, 1979: Fig. 152); *P. liosoma* (Ehrenberg, 1829) (specimens examined); *P. pallidus* Pocock, 1895 (specimen examined); *P. raudus* (Simon, 1887) (Lamoral, 1979: Fig. 178); *P. transvaalicus* Purcell, 1899 (specimen examined); *P. villosus* (Peters, 1861) (Lamoral, 1979: Fig. 202).

***Pseudolissothus*** Lourenço, 2001 (one species): ***DM<sub>c</sub>* visible:** *P. pusillus* Lourenço, 2001 (Lourenço, 2001f: Fig. 2F).

***Pseudolychas*** Kraepelin, 1911 (three species): ***DM<sub>c</sub>* visible:** *P. ochraceus* (Hirst, 1911) (Prendini, 2004b: Fig. 20); *P. pegleri* (Purcell, 1901) (Prendini, 2004b: Fig. 31); *P. transvaalicus* Lawrence, 1961 (Prendini, 2004b: Fig. 42).

\****Pseudouroplectes*** Lourenço, 1995b (one species): *P. betschi* Lourenço, 1995 (placed here since the genus is close to *Uroplectes*; Lourenço, 1995b).

***Tityobuthus*** Pocock, 1893 (12 species): ***DM<sub>c</sub>* visible:** *T. baroni* (Pocock, 1890) (Lourenço, 1996a: Fig. 49); *T. lucileae* Lourenço, 1996 (Lourenço, 1996a: Fig. 53); *T. rakotondravonyi* Lourenço et Goodman, 2003 (Lourenço & Goodman, 2003a: Fig. 27). ***DM<sub>c</sub>* not visible:** *T. antsingy* Lourenço et Goodman, 2004 (Lourenço & Goodman, 2004: Fig. 4); *T. darainensis* Lourenço et Goodman, 2002 (Lourenço & Goodman, 2002: Fig. 52). *T. dastychi* Lourenço, 1997 (Lourenço, 1997b: Fig. 5); *T. griswoldi* Lourenço, 2000 (Lourenço, 2000g: Fig. 20); *T. ivo-hibe* Lourenço et Goodman, 1999 (Lourenço & Goodman, 1999: Fig. 8); *T. manonae* Lourenço, 2000 (Lourenço, 2000g: Fig. 16); *T. monodi* Lourenço, 2000 (Lourenço, 2000g: Fig. 25); *T. pallidus* Lourenço, 2004 (Lourenço, 2004h: Fig. 2B); *T. pococki* Lourenço, 1995 (Lourenço, 1995a: Fig. 19).

***Troglobityobuthus*** Lourenço, 2000 (one species): ***DM<sub>c</sub>* visible:** *T. gracilis* (Fage, 1946) (Lourenço, 2000g: Fig. 7).

***Uroplectes*** Peters, 1861 (11 species): ***DM<sub>c</sub>* visible:** *U. gracilior* Hewitt, 1913 (Lamoral, 1979: Fig. 240);

*U. longimanus* Werner, 1936 (Lamoral, 1979: Fig. 247); *U. occidentalis* Simon, 1876 (Vachon, 1950b: Fig. 12; Lourenço, 2000h: Fig. 2D); *U. vittatus* (Thorell, 1876) (Fig. 17, specimen examined; specimen examined, traces of  $DM_c$  visible).  **$DM_c$  not visible:** *U. carinatus* (Pocock, 1890) (Lamoral, 1979: Fig. 213); *U. otjimbinguensis* (Karsch, 1879) (Lamoral, 1979: Fig. 256); *U. pilosus* (Thorell, 1876) (Lamoral, 1979: Fig. 264); *U. planimanus* (Karsch, 1879) (Lamoral, 1979: Fig. 272; specimen examined); *U. schlechteri* Purcell, 1901 (Lamoral, 1979: Fig. 280); *U. teretipes* Lawrence, 1966 (Lamoral, 1979: Fig. 287); *U. tumidimanus* Lamoral, 1979 (Lamoral, 1979: Fig. 295).

***Uroplectoides*** Lourenço, 1998 (one species):  **$DM_c$  not visible:** *U. abyssinicus* Lourenço, 1998 (Lourenço, 1998c: Fig. 3).

**"Tityus group". Trichobothrial pattern alpha; femur trichobothrium  $d_2$  located internally or absent (9 genera); tibial spurs absent (New World)**

***Alayotityus*** Armas, 1973; **femur trichobothrium  $d_2$  absent** (placed here due to general morphology and biogeographic connections) (five species):  **$DM_c$  visible:** *A. delacruzi* Armas, 1973 (Vachon, 1977: Fig. 1; Teruel, 2001a: Fig. 3); *A. gramma* Armas, 1984 (Armas, 1984: Fig. 3C); *A. juraguensis* Armas, 1973 (Armas, 1973: Fig. 9); *A. nanus* Armas, 1973 (Fig. 21, specimen examined); *A. sierramaestrae* Armas, 1979 (Lourenço & Vachon, 1996: Fig. 10; Lourenço, 1999b: Fig. 15).

***Centruroides*** Marx, 1890 (34 species):  **$DM_c$  visible:** *C. barbusensis* (Pocock, 1898) (Armas, 1983: Fig. 17A, 24A as *C. hummelincki*; Lourenço, 1984b: Fig. 10); *C. bicolor* (Pocock, 1898) (Francke & Stockwell, 1987: Fig. 17), specimen examined; *C. elegans* (Thorell, 1876), (specimen examined); *C. exilicauda* (Wood, 1863), (specimen examined); *C. exilimanus* Teruel et Stockwell, 2002 (Teruel & Stockwell, 2002: Fig. 14); *C. exsul* (Meise, 1934) (Sissom & Lourenço, 1987: Fig. 35); *C. gracilis* (Latrelle, 1804) (Sissom & Lourenço, 1987: Fig. 6; González-Sponga, 1996b: Fig. 287); *C. griseus* (C. L. Koch, 1844) (Francke & Sissom, 1980: Fig. 32; Armas, 1982: Fig. 4B, as *C. g. boringensis*); *C. hasethi* Pocock, 1902 (González-Sponga, 1996b: Fig. 290); *C. hentzi* (Banks, 1910), (specimen examined); *C. hoffmanni* Armas, 1996 (Armas, 1996: Fig. 6); *C. infamatus ornatus* Pocock, 1902, (specimen examined); *C. koesteri* Kraepelin, 1911 (Francke & Stockwell, 1987: Fig. 26; specimen examined); *C. limbatus* (Pocock, 1898) (Francke & Stockwell, 1987: Fig. 37; specimen examined); *C. limpidus* (Karsch, 1879), specimen examined; *C. lu-*

*ceorum* Armas, 1999 (Armas, 1999: Fig. 9C); *C. mahnerti* Lourenço, 1983 (Lourenço, 1983b: Fig. 9); *C. margaritatus* (Gervais, 1841) (Fig. 18, specimen examined; Francke & Stockwell, 1987: Fig. 46; Sissom & Lourenço, 1987: Figs. 19, 25); *C. melanodactylus* Teruel, 2001 (Teruel, 2001b: Fig. 11); *C. navarroi* Teruel, 2001 (Teruel, 2001b: Fig. 3); *C. nigrescens* (Pocock, 1898), specimen examined; *C. nigrovariatus baergi* Hoffmann, 1932, (specimen examined); *C. nitidus* (Thorell, 1877) (Schawaller, 1979: Fig. 6; as *C. beynai*, a fossil species from Dominican amber); *C. noxius* Hoffmann, 1932, (specimen examined); *C. pallidiceps* Pocock, 1902, (specimen examined); *C. pococki* Sissom et Francke, 1983 (Sissom & Francke, 1983: Fig. 5); *C. rileyi* Sissom, 1995 (Sissom, 1995: Fig. 23); *C. schmidti* Sissom, 1995 (Sissom, 1995: Fig. 14); *C. sculpturatus* Ewing, 1928, (specimen examined); *C. sissomi* Armas, 1996 (Armas, 1996: Fig. 2); *C. stockwelli* Teruel, 2001 (Teruel, 2001b: Fig. 22); *C. testaceus* (DeGeer, 1778) (Sissom & Francke, 1983: Fig. 17); *C. thorelli* Kraepelin, 1891 (Francke & Stockwell, 1987: Fig. 55; Sissom, 1995: Fig. 5); *C. vittatus* (Say, 1821), (specimen examined).

***Mesotityus*** González-Sponga, 1981 (one species):  **$DM_c$  visible:** *M. vondangeli* González-Sponga, 1981 (González-Sponga, 1981: Fig. 2; González-Sponga, 1996b: Fig. 301).

***Microtityus*** Kjellesvig-Waering, 1966 (nine species):  **$DM_c$  visible:** *M. ambarensis* (Schawaller, 1981) (Schawaller, 1981: Fig. 9; a fossil species from Dominican amber, as *Tityus ambarensis*); *M. biordi* González-Sponga, 1970 (González-Sponga, 1996b: Fig. 308); *M. dominicanensis* Santiago-Blay, 1985 (Santiago-Blay, 1985a: Fig. 6); *M. farleyi* Teruel, 2000 (Teruel, 2000: Fig. 2); *M. guantanamo* Armas, 1984 (Armas, 1984: Fig. 6B); *M. joseantonioi* González-Sponga, 1981 (González-Sponga, 1981: Fig. 11; González-Sponga, 1996b: Fig. 311); *M. starri* Lourenço et Huber, 1999 (Lourenço & Huber, 1999a: Fig. 17); *M. vanzolinii* Lourenço et Von Eickstedt, 1983 (Lourenço & Von Eickstedt, 1983b: Fig. 6); *M. waeringi* Francke et Sissom, 1980 (Francke & Sissom, 1980: Fig. 24).

***Rhopalurus*** Thorell, 1876 (two species):  **$DM_c$  visible:** *R. junceus* (Herbst, 1800) (Fig. 20, specimen examined); *R. laticauda* Thorell, 1876 (González-Sponga, 1996b: Fig. 317).

***Tityopsis*** Armas, 1974 (two species):  **$DM_c$  visible:** *T. aliciae* Armas et Martín Frías, 1998 (Armas & Martín Frías, 1998: Fig. 1B); *T. ineaqualis* (Armas, 1974) (Lourenço & Vachon, 1996: Fig. 16).

***Tityus*** C. L. Koch, 1836 (90 species):  **$DM_c$  visible:** *T. adisi* Lourenço et Pézier, 2002 (Lourenço & Pézier, 2002: Fig. 14); *T. adrianoi* Lourenço, 2003 (Lourenço, 2003g: Fig. 5); *T. anneae* Lourenço, 1997

(Lourenço, 1997a: Fig. 5); *T. antioquensis* Lourenço et Otero Patino, 1998 (Lourenço & Otero Patino, 1998: Figs. 2, 4); *T. apiacas* Lourenço, 2002 (Lourenço, 2002d: Figs. 2, 7); *T. arellanoparrai* González-Sponga, 1985 (González-Sponga, 1996b: Fig. 330); *T. bahiensis* (Perty, 1833) (Lourenço, 1982d: Fig. 9); *T. bahiensis eickstedtae* Lourenço, 1982 (Lourenço, 1982d: Fig. 6, as *T. eickstedtae*); *T. barquisimetanus* González-Sponga, 1994 (González-Sponga, 1996b: Fig. 407); *T. betschi* Lourenço, 1992 (Lourenço, 1992: Fig. 2); *T. blaseri* Mello-Leitão, 1931 (Lourenço et al., 1997: Fig. 3); *T. bocenoensis* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 395); *T. braziliæ* Lourenço et Von Eickstedt, 1984 (Lourenço & Von Eickstedt, 1984: Figs. 4, 11); *T. canopensis* Lourenço et Pézier, 2002 (Lourenço & Pézier, 2002a: Fig. 1); *T. carabobensis* González-Sponga, 1987 (González-Sponga, 1996b: Fig. 403). *T. cerroazul* Lourenço, 1986 (Lourenço, 1986b: Fig. 4); *T. championi* Pocock, 1898 (Francke & Stockwell, 1987: Fig. 69; specimen examined); *T. charreynoni* Vellard, 1932 (Lourenço, 1980b: Fig. 28, as *T. trivittatus charreynoni*; Lourenço, 2001i: Fig. 9); *T. clathratus* C. L. Koch, 1844 (Lourenço, 1983a: Fig. 21; González-Sponga, 1996b: Fig. 357); *T. columbianus* (Thorrell, 1876) (Lourenço, 1981: Fig. 7); *T. confluens* Borelli, 1899 (Lourenço, 1980: Fig. 40); *T. costatus* (Karsch, 1879) (Lourenço, 1980b: Fig. 22, as *T. trivittatus dorsomaculatus*; Lourenço & Giupponi, 2004: Figs. 5, 10); *T. culebreensis* González-Sponga, 1994 (González-Sponga, 1996b: Fig. 411); *T. dasyurus* Pocock, 1897 (Lourenço & Francke, 1984: Fig. 6; Santiago-Blay, 1985b: Fig. 5); *T. dedoslargos* Francke et Stockwell, 1987 (Francke & Stockwell, 1987: Fig. 78; specimen examined); *T. demangei* Lourenço, 1981 (Lourenço, 1981: Fig. 15); *T. dinizi* Lourenço, 1997 (Lourenço, 1997e: Fig. 5); *T. discrepans* (Karsch, 1879) (González-Sponga, 1996b: Fig. 324); *T. dupouyi* González-Sponga, 1987 (González-Sponga, 1996b: Fig. 348); *T. ecuadorensis* Kraepelin, 1896 (Lourenço, 1983c: Fig. 5; specimen examined); *T. elizabethae* Lourenço et Ramos, 2004 (Lourenço & Ramos, 2004: Fig. 13); *T. erikae* Lourenço, 1999 (Lourenço, 1999i: Fig. 3); *T. exstinctus* Lourenço, 1995 (Lourenço, 1995: Fig. 3); *T. falconensis* González-Sponga, 1974 (González-Sponga, 1996b: Fig. 383); *T. fasciolatus* Pessôa, 1935 (Lourenço, 1980b: Fig. 34, as *T. trivittatus fasciolatus*); *T. filodendron* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 339); *T. florezi* Lourenço, 2000 (Lourenço, 2000d: Fig. 9); *T. fuhrmanni* Kraepelin, 1914 (Lourenço, 1984a: Fig. 7); *T. fuenestus* Hirst, 1911 (González-Sponga, 1996b: Fig. 371); *T. gaffini* Lourenço, 2000 (Lourenço, 2000d: Fig. 2); *T. geratus* Santiago-Blay et Poinar, 1988 (Santiago-Blay & Poinar, 1988: Fig. 4; a fossil species from Dominican amber); *T. gasci* Lourenço, 1982 (Lourenço, 1982a: Fig. 5); *T. gonzalezspongai* Quiroga, De Sousa, Parrilla-Álvarez et Manzanilla: Quiroga et al., 2004: Figs. 3.2, 6.2); *T. insignis* (Pocock, 1889) (Lourenço, 1984e: Fig. 6, 16); *T. jeanvellardi* Lourenço, 2001 (Lourenço, 2001i: Fig. 26); *T. kuryi* Lourenço, 1997 (Lourenço, 1997c: Fig. 3); *T. lancinii* González-Sponga, 1972 (González-Sponga, 1996b: Fig. 379); *T. magnimanus* Pocock, 1897 (Lourenço, 1987: Fig. 8); *T. martinpaechi* Lourenço, 2001 (Lourenço, 2001e: Fig. 10); *T. matthieseni* Rocha et Lourenço, 2000 (Rocha & Lourenço, 2000: Fig. 5); *T. melanostictus* Pocock, 1893 (González-Sponga, 1996b: Fig. 360); *T. melici* Lourenço, 2003 (Lourenço, 2003c: Fig. 4); *T. meridanus* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 342); *T. metuendus* Pocock, 1897 (Lourenço, 1983d: Fig. 6); *T. monaguensis* González-Sponga, 1974 (González-Sponga, 1996b: Fig. 387); *T. munozi* Lourenço, 1997 (Lourenço, 1997c: Fig. 10); *T. nematochirus* Mello-Leitão, 1940 (Fig. 20, specimen examined; González-Sponga, 1996a: Figs. 79, 83; González-Sponga, 1996b: Fig. 333); *T. neoespartanus* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 1, 7); *T. nororientalis* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 11, 17); *T. obtusus* (Karsch, 1879) (Armas, 1977: Fig. 1C); *T. ocelote* Francke et Stockwell, 1987 (Francke & Stockwell, 1987: Fig. 87; specimen examined); *T. osmanus* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 22, 25); *T. pachyurus* Pocock, 1897 (Lourenço & Méndez, 1984: Fig. 6; Francke & Stockwell, 1987: Fig. 94); *T. paraensis* Kraepelin, 1896 (Lourenço, 1983a: Figs. 7, 13, as *T. cambridgei*); *T. parvulus* Kraepelin, 1914 (Lourenço, 1999g: Fig. 2); *T. perijanensis* González-Sponga, 1994 (González-Sponga, 1996b: Fig. 351); *T. pictus* Pocock, 1893 (Lourenço, 1984e: Fig. 24); *T. pittieri* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 327); *T. pococki* Hirst, 1907 (Lourenço, 1987: Fig. 19; González-Sponga, 1996a: Figs. 59, 64; González-Sponga, 1996b: Fig. 363); *T. potameis* Lourenço et Giupponi, 2004 (Lourenço & Giupponi, 2004: Figs. 22, 25); *T. prancei* Lourenço, 2000 (Lourenço, 2000d: Fig. 6); *T. pugilator* Pocock, 1898 (Lourenço, 1980a: Fig. 7, as *T. kraepelini*); *T. pusillus* Pocock, 1893 (Lourenço, 1982c: Fig. 5); *T. rebierei* Lourenço, 1997 (Lourenço, 1997d: Fig. 37); *T. riocaurensis* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 29, 35); *T. roigi* Maury et Lourenço, 1987 (Maury & Lourenço, 1987: Fig. 4); *T. rojasi* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 39, 45); *T. rugosus* Schenkel, 1932 (González-Sponga, 1996a: Figs. 69, 74; González-Sponga, 1996b: Fig. 367); *T. serrula-*

*tus* Lutz et Mello, 1922 (Lourenço & Von Eickstedt, 1983a: Fig. 5); *T. shiriana* González-Sponga, 1991 (González-Sponga, 1996b: Fig. 354); *T. silvestris* Pocock, 1897 (Lourenço, 1983a: Fig. 28); *T. suroorientalis* González-Sponga, 1996 (González-Sponga, 1996a: Figs. 49, 55); *T. tamayoi* González-Sponga, 1987 (González-Sponga, 1996b: Fig. 345); *T. trinitatis* Pocock, 1897 (Lourenço, 1984d: Fig. 3); *T. trivittatus* Kraepelin, 1898 (Lourenço, 1980b: Fig. 16); *T. unus* Pinto-da-Rocha et Lourenço, 2000 (Pinto-da-Rocha & Lourenço, 2000: Fig. 15); *T. urbinai* Scorza, 1952 (González-Sponga, 1996b: Fig. 336); *T. vaissadei* Lourenço, 2002 (Lourenço, 2002d: Fig. 18); *T. valerae* Scorza, 1954 (González-Sponga, 1996b: Fig. 375); *T. venamensis* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 399). *T. zulianus* González-Sponga, 1981 (González-Sponga, 1996b: Fig. 391). **DM<sub>c</sub> not visible:** *T. otero-roi* Lourenço, 1998 (Lourenço, 1998d: Figs. 2D, 3D).

***Troglorhopalurus*** Lourenço, Baptista et Giupponi, 2004 (one species): **DM<sub>c</sub> visible:** *T. translucidus* Lourenço, Baptista et Giupponi, 2004 (Lourenço et al., 2004a: Fig. 8).

***Zabius*** Thorell, 1893; **femur trichobothrium d<sub>2</sub> absent** (placed here due to general morphology and biogeographic connections) (three species): **DM<sub>c</sub> visible:** *Z. birabeni* Mello-Leitão, 1938; *Z. fuscus* (Thorell, 1876); *Z.* sp.n. (L. Acosta, pers. comm.).

### Exceptions

Although it is not our goal to evaluate the accuracy and/or artistic value of the figures examined in literature for this study, it is clear some scorpionsologists produced more exact and accurate figures than others, and, in some cases, these renderings over the years are not consistent for an author. Consequently, we have factored in our own unstated subjective opinions into the evaluation of these stated exceptions. We address each exception noted above by group and genus:

***Buthus* group.** 39 genera and 113 species, one exception: ***Buthacus*.** *B. ziegleri*, in Lourenço's (2000c: Fig. 6) figure, *d<sub>3</sub>* is depicted external to DM<sub>c</sub>.

***Ananteris* group.** Six genera and 39 species, four exceptions. ***Lychas*:** *L. mucronatus*: for this species, in Tikader & Bastawade's (1983: Fig. 150) figure trichobothria *d<sub>1</sub>–d<sub>5</sub>* are depicted quite high on the segment, all, including *d<sub>4</sub>*, positioned internal to the DM<sub>c</sub> carina. We find this configuration highly unlikely, especially the position of trichobothrium *d<sub>4</sub>* and therefore dismiss it from consideration. *L. rugosus*: in Tikader & Bastawade's (1983: Fig. 166) we note that trichobothrium *d<sub>4</sub>* is depicted external to the DM<sub>c</sub> carina and therefore cannot object to the figure on its surface value; *L. scaber*: in Tikader & Bastawade's (1983, Fig. 235)

figure both the *d<sub>3</sub>* and *d<sub>4</sub>* trichobothria are depicted as positioned internal to the DM<sub>c</sub> carina, we, again, dismiss this discrepancy due to the position of *d<sub>4</sub>*. *L. srilankensis*: in Lourenço's (1997f: Fig. 4) figure, *d<sub>3</sub>* is depicted internal to DM<sub>c</sub>.

***Isometrus* group.** Seven genera and 29 species, one exception. ***Isometrus*:** *I. vittatus*: in Tikader & Bastawade's (1983: Fig. 736) figure, trichobothria *d<sub>1</sub>* and *d<sub>2</sub>* are depicted internal to the dorsointernal (DI<sub>c</sub>) carina and both *d<sub>3</sub>* and *d<sub>4</sub>* internal to the DM<sub>c</sub> carina, clearly an unlikely configuration, and therefore, we dismiss this as an exception.

***Charmus* group.** Three genera and 7 species, no exceptions.

***Uroplectes* group.** 18 genera and 76 species, one exception: ***Butheoloides*.** *B. (Gigantoloides) aymerichi* in Lourenço's (2002e: Fig. 6) figure, *d<sub>3</sub>* is depicted internal to an apparent DM<sub>c</sub> carina. From the figure we see that trichobothrium *d<sub>3</sub>* is placed external to *d<sub>1</sub>* and *d<sub>4</sub>*, a typical alignment for this genus. The problem with the figure is the depiction of the DM<sub>c</sub> carina which bends considerably in an external direction at midsegment, almost reaching the DE<sub>c</sub> carina. Clearly this area of the "carina" must be extraneous granulation and therefore we dismiss it as an accurate depiction.

***Tityus* group.** Nine genera and 143 species, no exceptions.

In summary, out of seven stated exceptions we are left with three which we accept as plausible based solely on the figure as illustrated. This accounts for less than 1 % of the data gathered.

### Fossil buthoids (6 genera)

***Palaeolychas balticus*** Lourenço et Weitschat, 1996 (Lourenço & Weitschat, 1996: Fig. 5). Authors state: "tibia and chelae feebly carinate; all faces feebly granular". Our analysis based on figure and text: DM<sub>c</sub> presence unknown; beta pattern, *d<sub>2</sub>* not shown, not known if it is absent, undetected or has migrated to internal surface (which shows three trichobothria); 4–5 dorsal trichobothria shown on patella, *d<sub>3</sub>* positioned slightly towards external edge, somewhat external to segment midpoint; tibial spur present.

Assuming femoral trichobothrial *d<sub>2</sub>* has migrated to internal surface and considering the somewhat external position of patellar trichobothria *d<sub>3</sub>*, we can tentatively place this fossil scorpion in the ***Isometrus* group**.

***Palaeotityobuthus longiaculeus*** Lourenço et Weitschat, 2000. Femur and patella unknown; tibial spur absent.

***Palaeoprotobuthus pusillus*** Lourenço et Weitschat, 2000. Authors state: "Patella feebly carinate". DM<sub>c</sub> presence unknown; only one trichobothrium detectable on femur and four on patella, thus alpha/beta

pattern or patellar  $d_3$  position unknown; tibial spur absent.

***Palaeoakentrobuthus knodeli*** Lourenço et Weitschat, 2000 (Lourenço & Weitschat, 2000: Fig. 10). Authors state “tibia with five keels: one internal, 3 dorsal and 1 external”. We assume here the referenced carinae are  $DPS_c$ ,  $DI_c$ ,  $DM_c$ ,  $DE_c$ , and  $EM_c$  which are typically visible in Recent buthoids if the patella is viewed dorsally; *alpha* pattern with  $d_2$  apparently occurring on the dorsal surface; patellar trichobothrium  $d_3$  positioned on external half of segment; tibial spur present.

Assuming femoral trichobothrial  $d_2$  is located on dorsal surface and considering the somewhat external position of patellar trichobothria  $d_3$ , this fossil scorpion can be tentatively placed in the ***Charmus*** group.

***Palaeoananteris ribnitiodamgartensis*** Lourenço et Weitschat, 2001 (Lourenço & Weitschat, 2001: Fig. 2c). Authors state “tibia with 7 keels”; the figure shows the patella with a granulate carina with trichobothrium  $d_3$  situated slightly internal and  $d_4$  external. Based on the relative positions of the five dorsal trichobothria, we must assume the carina shown is  $DM_c$ ; femur reported with four dorsal trichobothria,  $d_2$  either undetected, absent, or positioned on internal surface, *alpha* pattern depicted; tibial spurs present.

Assuming Fig. 2c is correct and assumptions stated above are true, this is the only example of a buthoid with an *alpha* pattern and trichobothrium  $d_3$  positioned internal to the  $DM_c$  carina. Therefore, this fossil cannot be placed in any of the six hypothesized Recent buthoid groups.

***Uintascorpio*** Perry, 1995:  $DM_c$  carina visible (Santiago-Blay et al. 2004b: Fig. 5); trichobothria not visible nor the presence or absence of the tibial spurs is determinable.

## Cladistic Analysis

In this analysis we were interested primarily to see the effect of the new  $d_3$ - $DM_c$  alignment character as it related to the expanded *alpha/beta* definition as originally defined by Soleglad & Fet (2003b). It was very clear in Soleglad & Fet's (2003b) recent analysis of the *alpha/beta* pattern, which incorporated other primitive Recent scorpions and fossils, that this pattern was important phylogenetically in the upper-level analysis of the buthoids. It is obvious that Vachon (1975) also realized the importance of the *alpha/beta* pattern when he correlated all known buthoid genera and their biogeography with the *alpha/beta* pattern.

In an attempt to isolate other basic buthoid characters, using Sissom's (1990) key to buthoid genera as a basis, we decided to include the leg tibial spurs as well. The only other character used in the key that occurred in

several places was the “shape of the sternum”. However, based on the recent analysis of Soleglad & Fet (2003a), it is clear that the sternum “shape” is a bogus character and does not provide any meaningful phylogenetic information.

**Use of generic names as terminal tokens.** We need to stress here that the use of generic names as terminal taxa in the cladograms presented in this analysis, and analyses in previous publications for that matter (e.g., Soleglad & Fet, 2003b, etc.) does not necessarily imply monophyly of these genera. This should be particularly clear when, as in the case referenced above, the actual species set used for the cladistic analysis of that genus is *specifically stated*, and in many cases only one or two species were considered. It is clear that monophyly for a given genus can *only* be demonstrated if and only if a competent detailed species-level cladistic analysis is conducted which includes all species defined under that genus and select individuals from all immediate putative sister genera are included as outgroups; as for example, recently presented in Prendini's (2004b) impressive analysis of genus *Pseudolychas* which included all three species. Therefore, we emphasize here that the use of no less than 82 generic names in our cladograms in this paper certainly does not state or even imply that they are monophyletic.

## Character definitions

This analysis is based on six characters: two involving the pedipalp patella — the existence of the patellar  $DM_c$  carina, and the arrangement of trichobothrium  $d_3$  and carina  $DM_c$ ; three concerning the pedipalp femur — the angles formed by femoral trichobothria  $d_1-d_3$  and  $d_3-d_4$ , and the surface orientation of trichobothrium  $d_2$ ; and one involving the leg, the existence or absence of tibial spurs (legs III–IV or IV).

Note: for this study, we ignore the parallel alignment of femoral trichobothria  $d_1-d_3-d_4$  exhibited in genus *Liobuthus*, as well as the occasional absent and/or vestigial state of trichobothrium  $d_2$  in other species. Clearly, these derivations are autapomorphic to these taxa and therefore do not affect the overall results presented in this paper.

**Character 1:** Existence of the pedipalp patella dorsomedian ( $DM_c$ ) carina (*unordered*)

**0:** carina absent (*Archaeobuthus*, *Pseudochactas*)

**1:** carina present (all buthoids)

This character is included for two reasons: One, the character represents a synapomorphy for parvorder Buthida (or superfamily Buthoidea), as originally established by Soleglad & Fet (2003b), and two, it is directly relevant to the definition of character-2 below, the subject of this paper.

**Character 2:** Alignment of patella trichobothrium  $d_3$  with respect to the  $DM_c$  carina (*unordered*)

- 0:**  $d_3$  external to  $DM_c$  (*Ananteris, Isometrus, Charmus, Uroplectes*, and *Tityus* groups)
- 1:**  $d_3$  internal to  $DM_c$  (*Buthus* group)
- (-):** (*Archaeobuthus, Pseudochactas*)

As discussed below, we test four possible combinations of assigned polarity for this character using outgroup genus *Pseudochactas*. The result based on the state assignment of inapplicable (-) best represents, in our opinion, the most likely topology of the six hypothesized buthoid groups (Fig. 23). Different arguments for hypothesizing the plesiomorphic state of this character for the buthoids based on *Pseudochactas* are essentially equivocal. First, the  $DM_c$  carina does not exist in *Pseudochactas* and therefore, determining the position of trichobothrium  $d_3$  with respect to a non-existent carina can certainly be termed inapplicable in a cladistic sense. On the other hand, one could argue that, since the  $DM_c$  carina clearly evolved after the formation of the orthobothrioxic trichobothria in common to these two parvorders (Pseudochactida and Buthida), we can determine polarity based on the position of  $d_3$  on the segment in *Pseudochactas*, presumably more primitive than the buthoids. In Fig. 3, we see  $d_3$  located on the external half (i.e., towards the  $DE_c$  carina) of the patellar dorsal surface in this genus. From this we could conclude that “ $d_3$  external to  $DM_c$ ” is the most likely primitive state for the buthoids. However, one may argue also that we do not know what the effect of the derivation of a new carina has on the surface topology of the patella, maybe obscuring any localized positioning of a trichobothrium. In addition, one may argue that the trichobothria homology between the buthoids and *Pseudochactas* established by Soleglad & Fet (2001) is incorrect; that is, what we term as  $d_3$  across the two parvorders may not, in fact, be the same trichobothrium (i.e., originating from a single derivation). Arguments for state assignment “unknown” (?) can be given along the same lines as that presented for inapplicable (-) and, probably the least likely assignment, “ $d_3$  internal to  $DM_c$ ”, cannot be reasonably defended at all—we have no  $DM_c$  carina for reference and  $d_3$  is not located on the internal half (i.e., not closer to the  $DI_c$  carina) in *Pseudochactas*.

**Character 3:** Orientation of femoral trichobothria  $d_1-d_3$  with respect to dorsal carinae (*ordered*)

- 0:** parallel (*Archaeobuthus*)
- 1:**  $d_1-d_3$  angle towards the dorsoexternal carina (*beta*) (*Pseudochactas, Buthus, Ananteris*, and *Isometrus* groups)
- 2:**  $d_1-d_3$  angle towards the dorsointernal carina (*alpha*) (*Charmus, Uroplectes*, and *Tityus* groups)

This character represents one-half of the *alpha/beta* pattern and demonstrates the intermediate position of *Pseudochactas* between the fossil *Archaeobuthus* and the buthoids when combined with character-4. For this character *Pseudochactas* agrees with the *beta* pattern of the buthoids.

**Character 4:** Orientation of femoral trichobothria  $d_3-d_4$  with respect to dorsal carinae (*ordered*)

- 0:** parallel (*Archaeobuthus, Pseudochactas*)
- 1:**  $d_3-d_4$  angle towards the dorsointernal carina (*beta*) (*Buthus, Ananteris*, and *Isometrus* groups)
- 2:**  $d_3-d_4$  angle towards the dorsoexternal carina (*alpha*) (*Charmus, Uroplectes*, and *Tityus* groups)

For this character we see the primitive nature of *Pseudochactas*, complying with *Archaeobuthus*, thus showing that *Pseudochactas* is intermediate between *Archaeobuthus* and the buthoids (see character-3).

**Character 5:** Position of femoral trichobothrium  $d_2$  (*unordered*)

- 0:** located on dorsal surface (*Archaeobuthus, Pseudochactas, Buthus, Ananteris*, and *Charmus* groups)
- 1:** located on internal surface or dorsointernal carina (*Isometrus, Uroplectes*, and *Tityus* groups)

By simple inspection we can see that this character is incongruent with characters 3 and 4 (refer to Table 1). This incongruity is demonstrated in all four cladograms depicted in Figs. 23–25. We opted to model this character with a single derivation although it is clear that the migration of femoral trichobothrium  $d_2$  to the internal surface occurred separately in two clades, *Isometrus* group and *Uroplectes + Tityus* groups. For the former, based on available data, we detected a tendency of  $d_2$  occurring on the dorsointernal carina, implying, in a sense, a lesser dislocation of the trichobothrium. This slight distinction could provide rationale for two character states.

**Character 6:** Tibial spurs of legs (III–IV or IV) (*unordered*)

- 0:** spur present or sometimes vestigial (*Pseudochactas, Charmus* and *Uroplectes* groups, and most genera of *Buthus, Ananteris*, and *Isometrus* groups)
- 1:** spur absent (*Archaeobuthus*)
- 2:** spur absent (*Buthus* group: *Lanzatus, Liobuthus, Pectinibuthus, Plesiobuthus, Sabinebuthus, Vachoniolus*)
- 3:** spur absent (*Ananteris* group: *Akentrobuthus*)
- 4:** spur absent (*Isometrus* group: *Isometrus, Afroisometrus*)
- 5:** spur absent (*Tityus* group)

This somewhat irregular character, from a cladistic perspective, is included because we believe it is significant phylogenetically for the New World *Tityus* group, for reasons discussed elsewhere. Other occurrences, modeled as separate state derivations, are considered less important phylogenetically, many possibly the byproduct of specialized microhabitat adaptation. As suggested recently in Soleglad et al. (2005), the use of separate state values for similar looking derivations is a weaker assumption than assuming all such character changes occurred as a single derivation, and we adopt this approach here. Not only is it a weaker assumption, but equally as important, we do not believe these 19 occurrences of tibial spur losses are the product of a single evolutionary event and therefore, model these character states in accordance with the results based on the other characters. The presumed primitive state, tibial spurs being present, is based on their presence in many fossils, as well as in the most primitive Recent scorpion *Pseudochactas*.

### Character ordering

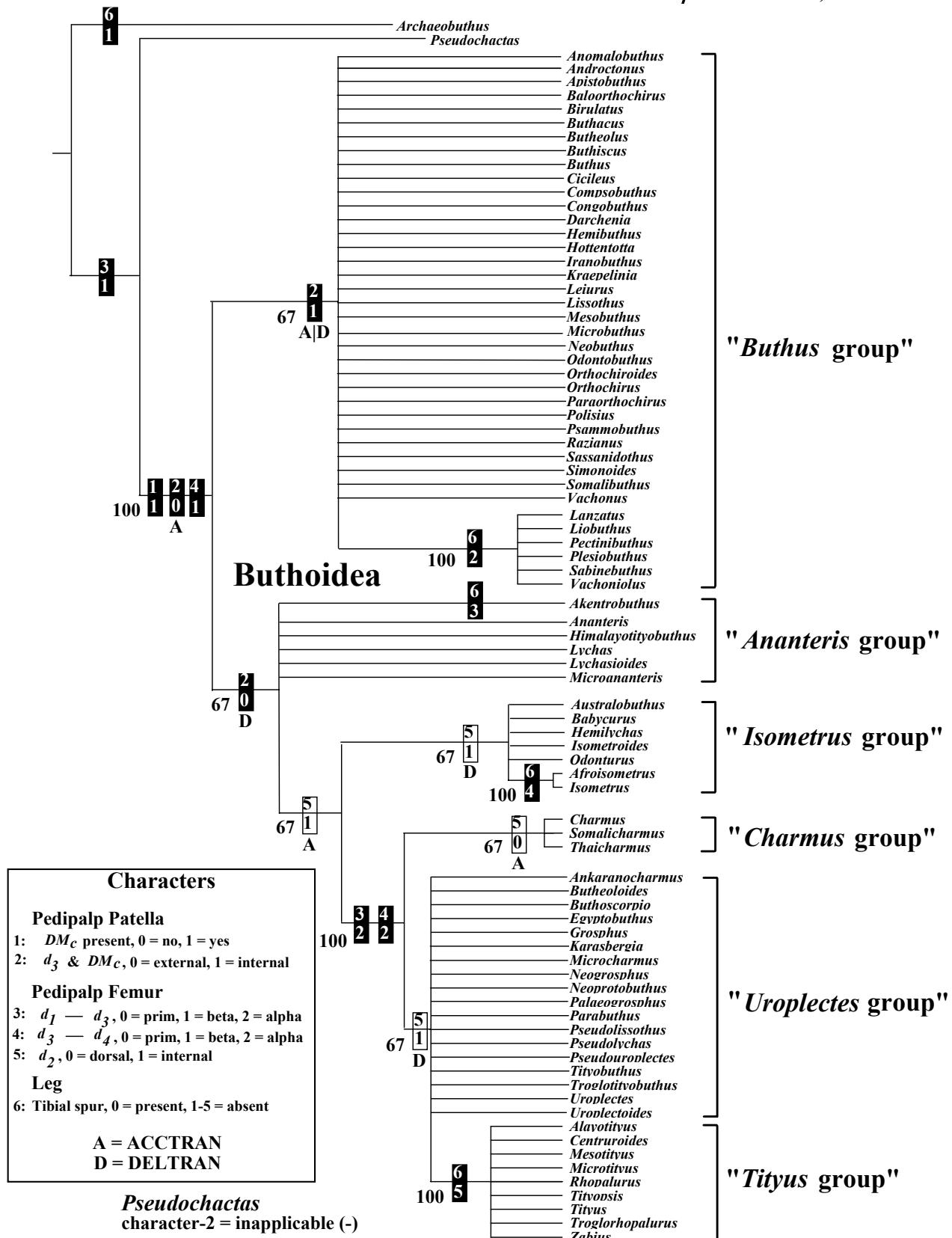
Characters 3 and 4, which define the angle direction of femoral trichobothria  $d_1-d_3$  and  $d_3-d_4$  with respect to the dorsal carinae, are ordered in this analysis. We ordered these two characters because we believe they do reflect the true evolution of the *alpha/beta* pattern which they represent (i.e., as they are distributed in the cladograms presented in Figs. 23–25). This belief is based on solid polarity information provided by the outgroup taxa, the fossil *Archaeobuthus* and the primitive Recent scorpion *Pseudochactas*: (1) *Pseudochactas* is intermediate between *Archaeobuthus* and the buthoids by exhibiting only “one-half” of the *beta* pattern (character-3), while being consistent with *Archaeobuthus* in character-4; and, (2) this is further supported by the dorsal placement of trichobothrium  $d_2$  in the two outgroup taxa, a *beta* pattern characteristic. In addition, these two characters exhibit congruency with the patella  $d_3-DM_c$  character (character-2) described in detail in this paper. In Soleglad & Fet (2003b), these two characters were not ordered.

We might add here that we obtain the same topology as shown in Figs. 23–25 and overall tree support data when these characters are not ordered. The only differences in the four combinations of character-2 assignment to *Pseudochactas* (see Table 2) is the number of resulting MPTs: ten MPTs instead of nine for inapplicable (-) and unknown (?) assignments, and four MPTs instead of three for “ $d_3$  external to  $DM_c$ ” assignment. The percentage of tree support for majority-rule consensus is essentially the same for these different MPT counts, 67 % being replaced with 60–70 % in the ten MPT case and 67 % being replaced with 75 % in the four MPT case.

### Results

We exercised four separate cladistic sequences spanning all possible combinations of hypothesized polarity for the new character,  $d_3-DM_c$  (character-2). In particular, we used the outgroup genus *Pseudochactas* as a vehicle for assigning polarity of this character to the buthoids. As discussed above, this approach is necessary because neither of the two outgroups exhibit the  $DM_c$  carina and therefore one cannot establish its polarity with any certainty. Plausible arguments supporting each one of these assignments are presented above under the description of this character.

Figure 23 presents the topology and a complete detailed breakdown of all buthoid genera for the case where character-2 is assigned an inapplicable (-) state value to *Pseudochactas*. We used the topology presented in this cladogram as the basis for the groups of genera proposed in this paper. It is important to note here that two of these groups, the *Ananteris* group and the *Uroplectes* group, are not supported as monophyletic groups; that is, this limited character set does not provide any synapomorphies for these clades. The other four groups are supported by at least two-thirds of the trees (six out of nine): the parvorder Buthida (or superfamily Buthoidea) is supported by all trees, two of the characters providing unambiguous synapomorphies, character-1 (state = 1), derivation of the  $DM_c$  carina, and character-4 (state = 1), completion of the *beta* pattern. Clade (*Charmus* group + *Uroplectes* group + *Tityus* group) is also supported by all trees, with two unambiguous synapomorphies, character-3 (state = 2) and character-4 (state = 2), representing the *alpha* pattern. The *Buthus* group node is supported by two-thirds of the trees with an ambiguously distributed character-2 (state = 1,  $d_3$  internal to  $DM_c$ ), a potential synapomorphy. Note that six genera in this group form a clade based on the absence of the tibial spur (character-6, state = 2); however, we consider this clade to be artificial and therefore it most probably does not represent a monophyletic group. The clade (*Ananteris* group + (*Isometrus* group + (*Charmus* group + (*Uroplectes* group + *Tityus* group)))) is supported by two-thirds of the trees and represents an interesting ladderization of these groups. This clade is distinguished from the *Buthus* group by character-2 (state = 0,  $d_3$  external to  $DM_c$ ), which forms a potential synapomorphy. This clade includes both *beta* and *alpha* scorpions. The outside clade, the *Ananteris* group, represents a “pure” form of the *beta* scorpions, with femoral trichobothrium  $d_2$  located on the dorsal surface. The next clade in this ladderization, the *Isometrus* group, represents a modified *beta* pattern, closer to the *alpha* pattern with  $d_2$  located either on the dorso-internal carina or the internal surface. Continuing, the next clade, (*Charmus* group + (*Uroplectes* group + *Tityus* group)), represents *alpha* scorpions, with  $d_2$  posi-



**Figure 23:** Cladogram showing majority-rule consensus of 9 MPTs for upper-level phylogeny of superfamily Buthoidea with characters distributed. Assumes character-2 (trichobothrium  $d_3$  position with respect to  $DM_c$  carina) as inapplicable (-) for *Pseudochactas*. Six partially defined clades are identified by the name of the group of genera. Characters 3 and 4 are ordered. Ambiguous character distribution is identified with the A(ACCTRAN) and/or D(DELTRAN) designation. Consensus tree support (a percentage) is presented under each branch. Tree support: length/CI/RI/G-Fit = 14/0.9286/0.9931/-5.750. Open rectangles depict homoplasious characters. Character number depicted on top and character state on bottom.

tion variable. In the *Charmus* group,  $d_2$  is located on the dorsal surface, a *beta* characteristic. Finally, for the clade (*Uroplectes* group + *Tityus* group), we see the pure form of the *alpha* pattern,  $d_2$  located on the internal surface of the femur. What is particularly inviting about the ladderization of the clade identified by  $d_3$  external to  $DM_c$ , is the gradual change from a pure *beta* form, as seen in the *Ananteris* group, to the pure *alpha*, as exhibited in the clade (*Uroplectes* group + *Tityus* group), with the *Isometrus* and *Charmus* groups forming intermediate stages. Of course, it must be stressed here that this topology is based only on six characters.

Figure 24 depicts the topology when character-2 is assigned an unknown (?) state to *Pseudochactas*. Except for the minor distributional changes for character-2 (state = 0), the result is identical to the previous topology discussed in detail, including consensus support and overall tree support data.

Figure 25 presents two cladograms where we specifically assigned a state value to *Pseudochactas* for character-2: trichobothrium  $d_3$  located *external* to the (nonexistent)  $DM_c$  carina and, trichobothrium located *internal* to the carina. Predictively, for the case where we assume  $d_3$  external to  $DM_c$  as primitive to the buthoids, we see  $d_3$  internal to  $DM_c$  as an unambiguous synapomorphy for the *Buthus* group and the clade (*Ananteris* group + (*Isometrus* group + (*Charmus* group + (*Uroplectes* group + *Tityus* group)))) is not supported. In contrast, if we assume  $d_3$  internal to  $DM_c$ , then the *Buthus* group is undefined and the clade (*Ananteris* group + (*Isometrus* group + (*Charmus* group + (*Uroplectes* group + *Tityus* group)))) is defined unambiguously. Of course, all other clades discussed above under different assumptions (Figs. 23 and 24) remain the same.

The overall support data is quite high for this minimal character set, with only one character, character-5, exhibiting homoplasy, resulting in length/Consistency Index (CI)/Retention Index (RI)/Goloboff-Fit (G-Fit) = 14/0.9286/0.9932/-5.750 (see Kitching et al., 1998, for definition of terms). Table 2 shows the majority-rule consensus for all four cladistic sequences where we see consistency across these sequences in those clades where 100 % MPTs are found, or where no support is exhibited. Predictively, the two clades that are delineated by the location of  $d_3$  with respect to  $DM_c$  (character-2) are contrasted with either 100 % support or no support depending on the assigned polarity via *Pseudochactas*.

### Character distribution

We present the distribution of character derivations of the four cladistic sequences discussed above for all clades resulting in these analyses (see cladograms in Figs. 23–25, identified in this section as 1, 2, 3, and 4, respectively, for location of these nodes). Each derivation (a potential synapomorphy) is described as follows:

*character\_number* (*old\_state* = *value1* → *new\_state* = *value2*,  $\bar{U}$ (*n*ambiguous) | *A*(CCTRAN only) | *D*(ELTRAN only), *valid\_sequences*) followed by a brief verbal description. *Value1* and *value2* = 0 - n|(-) = integer|inapplicable; *valid\_sequences* = which cladistic sequences comply (1, 2, 3, and/or 4). Consult the discussion above for a detailed description of referenced characters and their state values.

***Archaeobuthus*.** Character 6 (state=0 → state=1, U, 1–4): tibial spurs absent (lost).

***Pseudochactas* + *Buthida*.** Character 2 (state=(-) → state=0, A, 2): patellar trichobothrium  $d_3$  external to  $DM_c$ ; Character 3 (state=0 → state=1, U, 1–4): femoral trichobothria  $d_1$ – $d_3$  angles towards  $DE_c$ .

***Buthida*.** Character 1 (state=0 → state=1, U, 1–4): patellar  $DM_c$  carina present; Character 2 (state=(-) → state=0, A, 1): patellar trichobothrium  $d_3$  external to  $DM_c$ ; Character 4 (state=0 → state=1, U, 1–4): femoral trichobothria  $d_3$ – $d_4$  angles towards  $DI_c$ .

***Buthus* group.** Character 2 (state=(-)|0 → state=1, A|U, 1,2|3): patellar trichobothrium  $d_3$  internal to  $DM_c$ .

***Lanzatus* + *Liobuthus* + *Pectinibuthus* + *Plesiobuthus* + *Sabinebuthus* + *Vachoniolus*.** Character 6 (state=0 → state=2, U, 1–4): tibial spurs absent (lost). [Note that this clade is considered artificial]

***Ananteris* + *Isometrus* + *Charmus* + *Uroplectes* + *Tityus* groups.** Character 2 (state=(-)|0 → state=0, D|U, 1,2|4): patellar trichobothrium  $d_3$  external to  $DM_c$ .

***Ananteris* group.** No character support, all sequences.

***Akentrobuthus*.** Character 6 (state=0 → state=3, U, 1–4): tibial spurs absent (lost).

***Isometrus* + *Charmus* + *Uroplectes* + *Tityus* groups.** Character 5 (state=0 → state=1, A, 1–4): femoral trichobothrium  $d_2$  located on  $DI_c$  or internal surface.

***Isometrus* group.** Character 5 (state=0 → state=1, D, 1–4): femoral trichobothrium  $d_2$  located on  $DI_c$  or internal surface.

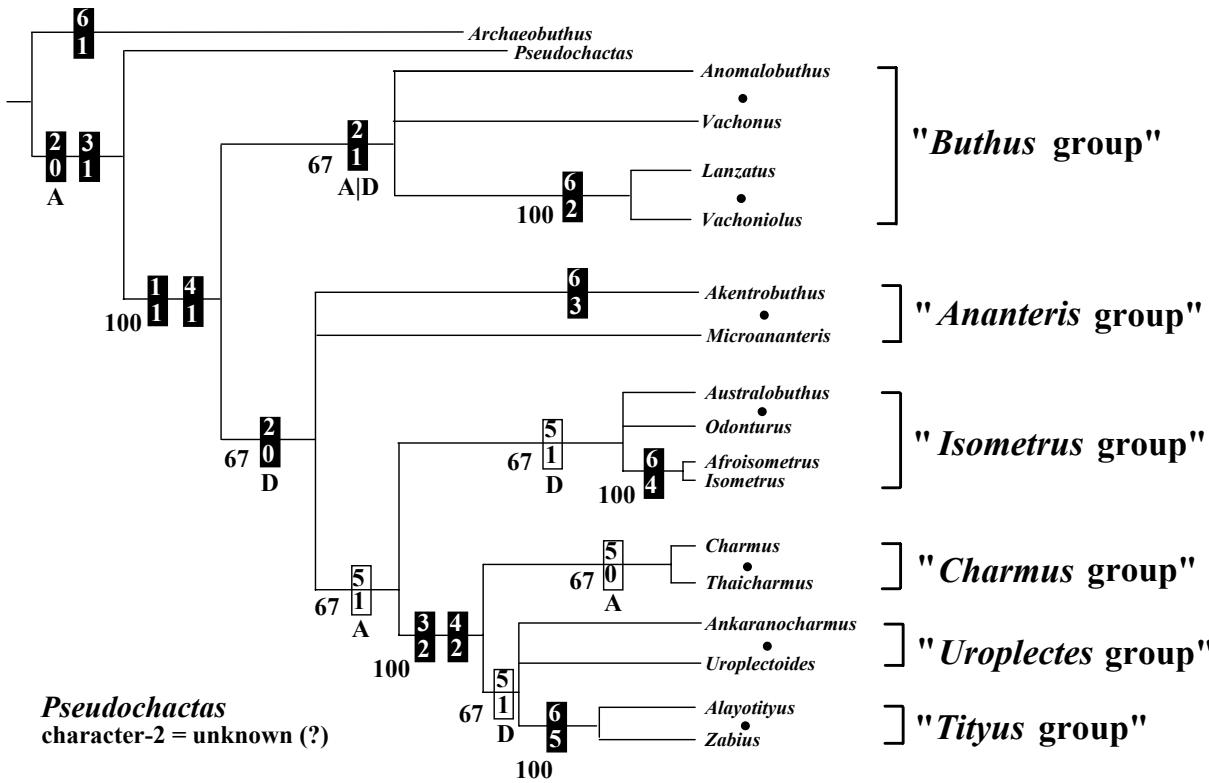
***Afroisometrus* + *Isometrus*.** Character 6 (state=0 → state=4, U, 1–4): tibial spurs absent (lost).

***Charmus* + *Uroplectes* + *Tityus* groups.** Character 3 (state=1 → state=2, U, 1–4): femoral trichobothria  $d_1$ – $d_3$  angles towards  $DI_c$ ; Character 4 (state=1 → state=2, U, 1–4): femoral trichobothria  $d_3$ – $d_4$  angles towards  $DE_c$ .

***Charmus* group.** Character 5 (state=1 → state=0, A, 1–4): femoral trichobothrium  $d_2$  located on dorsal surface.

***Uroplectes* + *Tityus* groups.** Character 5 (state=0 → state=1, D, 1–4): femoral trichobothrium  $d_2$  located on internal surface.

***Uroplectes* group.** No character support, all sequences.



**Figure 24:** Cladogram showing majority-rule consensus of 9 MPTs for upper-level phylogeny of superfamily Buthoidea with characters distributed. Assumes character-2 (trichobothrium  $d_3$  position with respect to  $DM_c$  carina) as unknown (?) for *Pseudochactas*. Six partially defined clades are identified by the name of the *group of genera* (see Fig. 23 for group contents and character definitions). Characters 3 and 4 are ordered. Ambiguous character distribution is identified with the A(CCTRAN) or D(ELTRAN) designation. Consensus tree support (a percentage) is presented under branch. Open rectangles depict homoplasious characters. Character number depicted on top and character state on bottom.

**Tityus group.** Character 6 (state=0 → state=5, U, 1–4): tibial spurs absent (lost).

**Homoplasy**

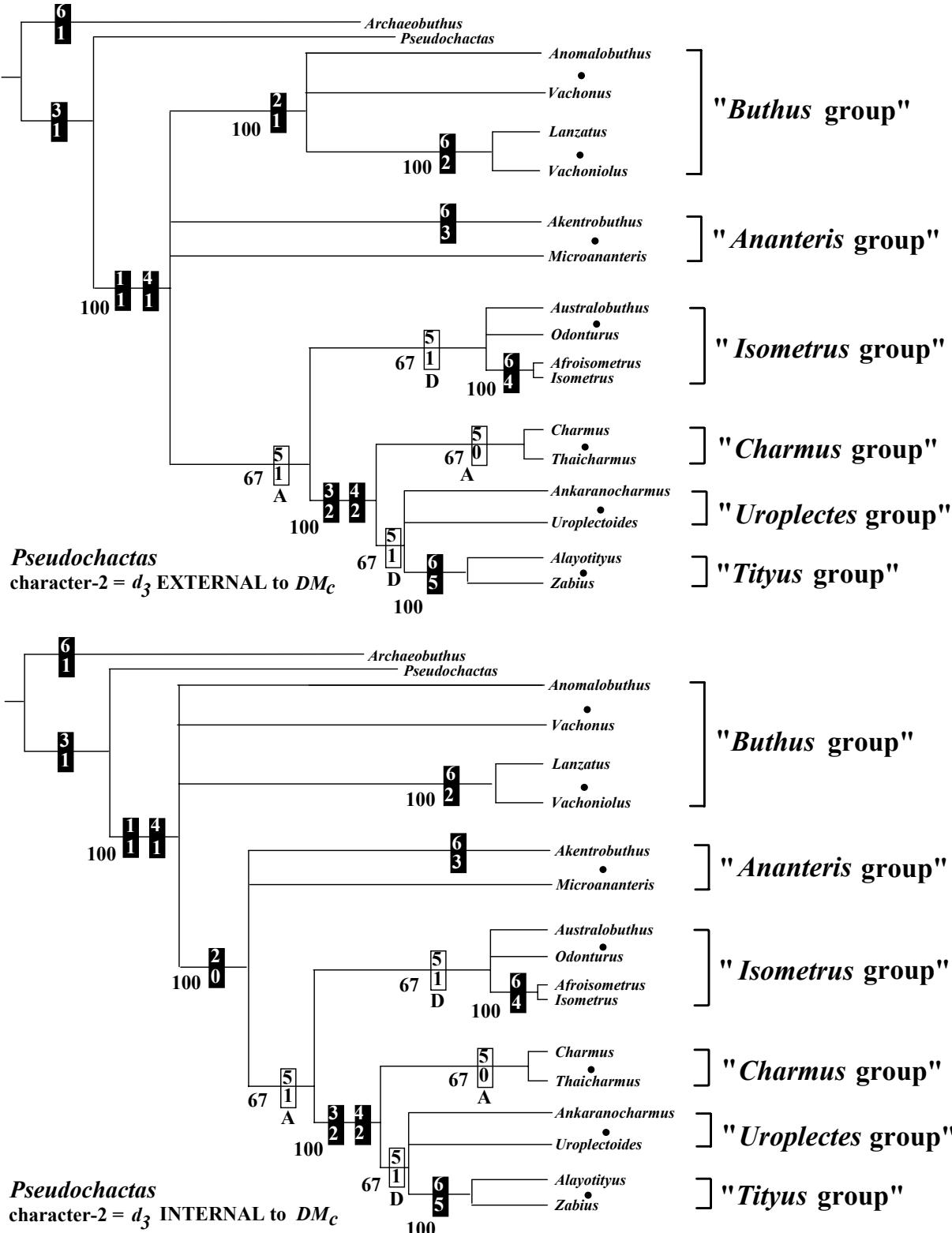
**Tites group + Tityus group)), and a reversal in the Charmus group,** the trichobothrium migrating “back” to the dorsal surface.

Since the location of  $d_2$  in the **Isometrus group** is somewhat equivocal between the dorsointernal carina and the internal surface, whereas, in the clade (**Uroplectes group + Tityus group**), we see a more consistent internal surface location, we consider these as separate derivations, which probably should be given separate state values. We believe that this scenario is more plausible than a reversal in the **Charmus group**. Therefore, for any subsequent buthoid analysis, we strongly recommend that these two instances of internal location of trichobothrium  $d_2$  be assigned separate character states (it is also, by the way, a weaker assumption).

### Buthoid group definitions

We consolidate the six suggested buthoid groups in this section by providing diagnoses based on the small character set evaluated in this paper. We also sketch out their biogeographical affinities. See Table 1 for a list of genera assigned to these six groups, representing all 82 genera currently assigned to superfamily Buthoidea. In

Character-5, the position of femoral trichobothrium  $d_2$ , is the only character that exhibits homoplasy (CI = 0.500). This character is incongruent with characters 3 and 4, the orientation of trichobothria  $d_1$ ,  $d_3$ , and  $d_4$ . From a pure cladistic perspective, the homoplasy was reflected in character-2 instead of characters 3 and 4 simply for reasons of parsimony, a smaller number of steps to resolve the incongruity (i.e., if characters 3 and 4 were stipulated as homoplasious, we would have an additional step). Based on the distribution of character-2 (see Figs. 23–25 and distribution discussion above) we see two solutions to this incongruity: (1) for “delayed optimization”, we see the derivation to the internal surface occurring twice, in the **Isometrus group**, a *beta* scorpion group, and in the (**Uroplectes group + Tityus group**) clade, both *alpha* scorpion groups; and (2) for “accelerated optimization”, we again see two derivations, migration to the internal surface at the node separating (**Isometrus group + (Charmus group + (Uroplectes group + Tityus group))**), and a reversal in the **Charmus group**, the trichobothrium migrating “back” to the dorsal surface.



**Figure 25:** Cladograms showing majority-rule consensus of 3 MPTs for upper-level phylogeny of superfamily Buthoidea with characters distributed. Top cladogram assumes trichobothrium  $d_3$  is located external to (the nonexistent)  $DM_c$  carina in *Pseudochactas*; bottom cladogram assume trichobothrium is located internal to  $DM_c$  carina. Six partially defined clades are identified by the name of the group of genera (see Fig. 23 for group contents and character definitions). Characters 3 and 4 are ordered. Ambiguous character distribution is identified with the A(CCTRAN) or D(ELTRAN) designation. Consensus tree support (a percentage) is presented under branch. Open rectangles depict homoplasious characters. Character number depicted on top and character state on bottom.

the diagnoses, we list synapomorphies, potential synapomorphies (i.e., ambiguously distributed characters), and symplesiomorphies. Note, in two cases, only symplesiomorphies compose the diagnosis (i.e., the groups are not phylogenetically defined).

***Buthus* group.** Diagnosis: femoral trichobothrium  $d_2$  located on dorsal surface; femoral trichobothria  $d_1-d_3$  angles towards  $DE_c$ ; femoral trichobothria  $d_3-d_4$  angles towards  $DI_c$ ; patellar trichobothrium  $d_3$  internal to  $DM_c$ ; tibial spurs are predominantly present. Geographical distribution: 39 genera: predominantly Palearctic genera, a few species spread to adjacent zones in Afrotropical and Oriental regions; no Neotropical, southern Afrotropical, Madagascar, or Australian forms.

***Ananteris* group.** Diagnosis (no synapomorphies): femoral trichobothrium  $d_2$  located on dorsal surface; femoral trichobothria  $d_1-d_3$  angles towards  $DE_c$ ; femoral trichobothria  $d_3-d_4$  angles towards  $DI_c$ ; patellar trichobothrium  $d_3$  external to  $DM_c$ ; tibial spurs are predominantly present. Geographical distribution: six genera: one Afrotropical-Neotropical (*Ananteris*) and one closely related Neotropical (*Microananteris*); one widely ranging Afrotropical-Oriental-Australian (*Lychas*); two Afrotropical (*Lychasioides*, *Akentrobuthus*); and one Oriental (*Himalayotityobuthus*).

***Isometrus* group.** Diagnosis: femoral trichobothrium  $d_2$  located on internal surface or dorsointernal carina; femoral trichobothria  $d_1-d_3$  angles towards  $DE_c$ ; femoral trichobothria  $d_3-d_4$  angles towards  $DI_c$ ; patellar trichobothrium  $d_3$  external to  $DM_c$ ; tibial spurs are predominantly present. Geographical distribution: seven genera: three Afrotropical (*Afroisometrus*, *Babycurus*, *Odonturus*); three Australian (*Australobuthus*, *Hemilychias*, *Isometroides*); one widely ranging Afrotropical-Oriental-Australian (*Isometrus*). No Neotropical forms.

***Charmus* group.** Diagnosis: femoral trichobothrium  $d_2$  located on dorsal surface; femoral trichobothria  $d_1-d_3$  angles towards  $DI_c$ ; femoral trichobothria  $d_3-d_4$  angles towards  $DE_c$ ; patellar trichobothrium  $d_3$  external to  $DM_c$ ; tibial spurs are predominantly present. Geographical distribution: a closely related group of three genera, Oriental (*Charmus*, *Thaicharmus*) and Afrotropical (*Somalicharmus*). No Neotropical or Australian forms.

***Uroplectes* group.** Diagnosis (no synapomorphies): femoral trichobothrium  $d_2$  located on internal surface; femoral trichobothria  $d_1-d_3$  angles towards  $DI_c$ ; femoral trichobothria  $d_3-d_4$  angles towards  $DE_c$ ; patellar trichobothrium  $d_3$  external to  $DM_c$ ; tibial spurs are predominantly present. Geographical distribution: 18 genera; eight are Afrotropical (*Butheoloides*, *Egyptobuthus*, *Karasbergia*, *Parabuthus*, *Pseudolissothus*, *Pseudolychias*, *Uroplectes*, *Uroplectoides*); nine are Madagascar endemics (*Ankaranocharmus*, *Grosphus*, *Microcharmus*, *Neogrosphus*, *Neoprotobuthus*, *Palaeogrosphus*, *Pseudouroplectes*, *Tityobuthus*, *Troglotityobuthus*); one Ori-

tal (*Buthoscorpion*). No Neotropical or Australian forms. Note that the Madagascar genera also include those currently separated under the family Microcharmidae (*Ankaranocharmus*, *Microcharmus*, *Neoprotobuthus*); however, this placement does not indicate that we endorse here the formal synonymy of Microcharmidae with Buthidae.

***Tityus* group.** Diagnosis: femoral trichobothrium  $d_2$  located on internal surface; femoral trichobothria  $d_1-d_3$  angles towards  $DI_c$ ; femoral trichobothria  $d_3-d_4$  angles towards  $DE_c$ ; patellar trichobothrium  $d_3$  external to  $DM_c$ ; tibial spurs absent. Geographical distribution: 9 genera; all Neotropical.

## Historical biogeography

The following observations can be made regarding the historical biogeography of buthoid groups of genera separated in our phylogenetic trees.

The numerous ***Buthus*** group includes 39 predominantly arid-adapted Palearctic genera, many endemic to southern parts of the Palearctic region (especially North Africa and Middle East). Some of these genera lost tibial spurs, probably several times. The most recent common ancestor of this group probably had a Laurasian origin, and the observed arid-adapted radiation could have been a Tertiary event. However, the lineage itself clearly represents one of the two major, ancient surviving clades with their roots likely in Pangea.

The second clade encompasses 43 genera separated into five groups. These are predominantly Afrotropical genera; very few of them are spread across Afrotropical, Oriental, and Australian regions (*Lychas*, *Isometrus*). It includes also a few Oriental and Australian genus-level endemics, and a separate Neotropical clade of nine genera. The modern Afrotropical region appears to be the major center of diversity for this buthoid clade, and it could be also its center of origin.

The important Oligocene Baltic amber fossils (ca. 60 Mya) exhibit features of at least three genera groups not found currently in the northern fragments of Pangea. Therefore, we can assume that several ancient buthoid groups were present in both Laurasian and Gondwanan parts as late as in the Tertiary, thus surviving the K-T extinction. The evidence for this are the genera *Palaeolychias* (which can be tentatively placed in the ***Isometrus*** group), *Palaeoakentrobuthus* (which can be tentatively placed in the ***Charmus*** group), and *Palaeoananteris* (which appears to belong to an extinct buthoid lineage). The extinction of these arboreal (found in amber) groups with the increased Tertiary aridization in the Palearctic region and subsequent Pleistocene glaciations seems a very realistic scenario.

The ***Ananteris*** group (six beta genera) presents an interesting, relict, and probably non-monophyletic assemblage surviving now only in some fragments of

	Inapplicable (-)	Unknown (?)	$DM_c / d_3$ Primitive	$d_3 / DM_c$ Primitive	Total Support
<b><i>Buthus</i> group</b>	6 (67 %)	6 (67 %)	<b>3 (100 %)</b>	<b>0</b>	15 (63 %)
<b><i>Ananteris</i> group</b>	0	0	0	0	0
<b><i>Isometrus</i> group</b>	6 (67 %)	6 (67 %)	2 (67 %)	2 (67 %)	16 (67 %)
<b><i>Charmus</i> group</b>	6 (67 %)	6 (67 %)	2 (67 %)	2 (67 %)	16 (67 %)
<b><i>Uroplectes</i> group</b>	0	0	0	0	0
<b><i>Tityus</i> group</b>	9 (100 %)	9 (100 %)	3 (100 %)	3 (100 %)	24 (100 %)
<b><i>A + I + C + U + T</i></b>	6 (67 %)	6 (67 %)	<b>0</b>	<b>3 (100 %)</b>	15 (63 %)
<b><i>I + C + U + T</i></b>	6 (67 %)	6 (67 %)	2 (67 %)	2 (67 %)	16 (67 %)
<b><i>C + U + T</i></b>	9 (100 %)	9 (100 %)	3 (100 %)	3 (100 %)	24 (100 %)
<b><i>U + T</i></b>	6 (67 %)	6 (67 %)	2 (67 %)	2 (67 %)	16 (67 %)

**Table 2:** Tree data (majority-rule consensus) supporting the monophyly of the six hypothesized buthoidea groups based on all possible combinations of polarity assignments for the  $d_3 - DM_c$  character as assigned to outgroup genus *Pseudochactas*: Inapplicable (-), unknown (?), trichobothrium  $d_3$  is aligned *external* to the  $DM_c$  carina, and  $d_3$  is aligned *internal* to the  $DM_c$  carina. Data specifies number of trees (and their percentage (%)) of all trees) supporting monophyly of each clade. Note, there is no support for the *Ananteris* and *Uroplectes* groups, whereas the other groups are supported at least by 63 % of the trees. White on black data areas show the two clades that are affected by the polarity of this character, exhibiting either 0 % or 100 % support, depending on the polarity assignment. *A* = *Ananteris* group, *I* = *Isometrus* group, *C* = *Charmus* group, *U* = *Uroplectes* group, *T* = *Tityus* group.

Gondwanaland, with an especially interesting Afrotropical-Neotropical genus *Ananteris*. The genus *Lychas* is very common and widespread in the Oriental region. Notably, none of the genera in this group evolved any adaptations to arid habitats.

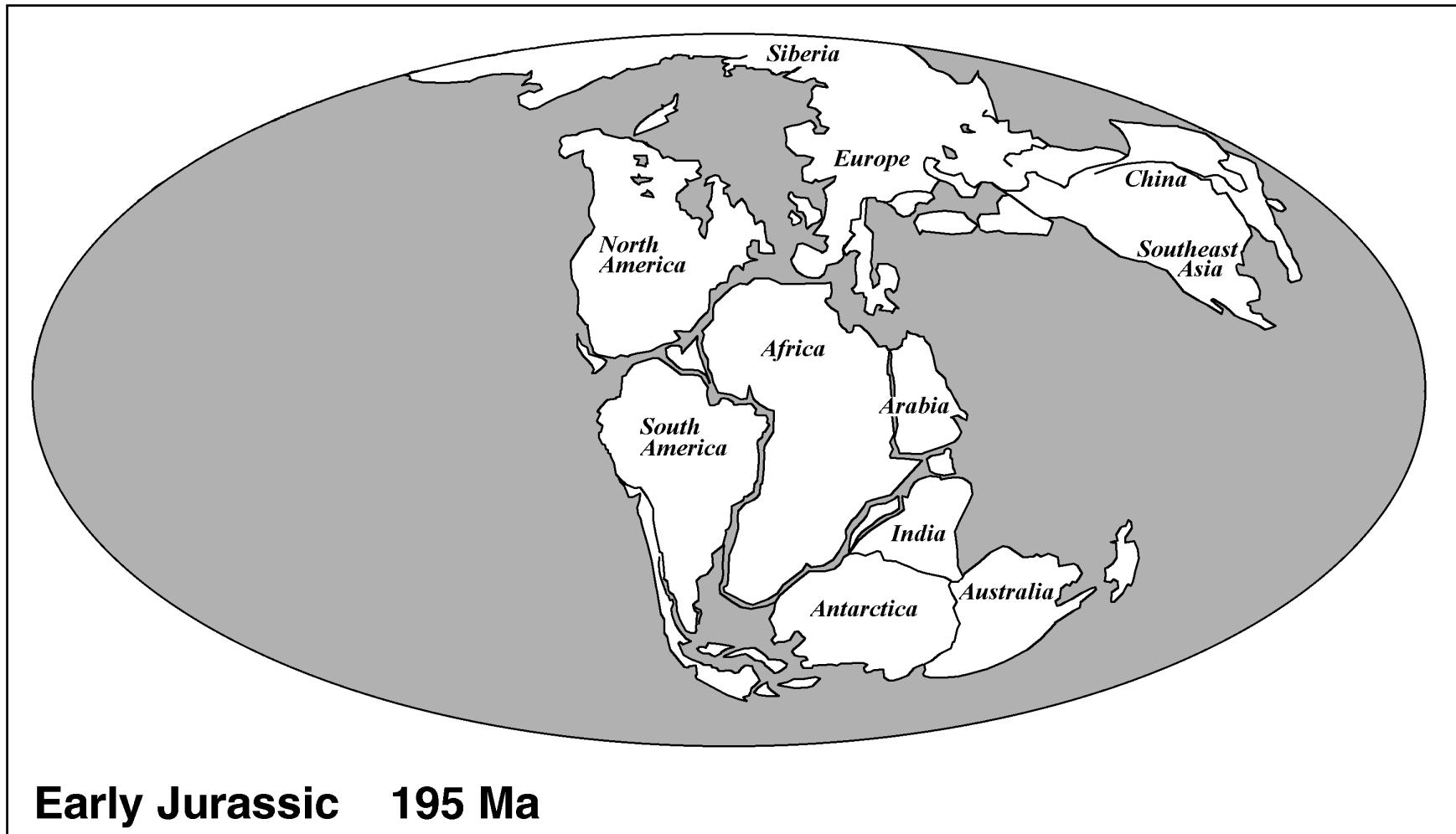
The *Isometrus* group (seven *beta* genera) also appears to include an assemblage of relict origin: four Afrotropical and three Australian genera, and one widely ranging genus of presumable Oriental origin (*Isometrus*). Among these genera, *Afroisometrus* and *Isometrus* lost tibial spurs.

The remaining three groups represent a clade with *alpha* configuration (Vachon, 1975), a clear synapomorphy of 30 buthoid genera, mostly Afrotropical (18) and Neotropical (nine); the group includes four Oriental and no Australian forms. The origin of this clade probably predates the fragmentation of Gondwanaland, judging from the information presented below.

A small *Charmus* group of two Oriental and one Afrotropical genera forms an outgroup to the final clade of (*Uroplectes* group + *Tityus* group). The large *Uroplectes* group (monophyly of which, however, is not confirmed) encompasses 18 genera, all found in the Old World; eight of these genera are Afrotropical; nine are Madagascar endemics, including all three genera of Microcharmidae; and one is Oriental (*Buthoscorpio*). The fact that all endemic Madagascar buthoids are nested within this Afrotropical-Oriental group indicates that most buthoid groups discussed here should have evolved long before the separation of Madagascar (and India) from the African plate. Separation of the block including Madagascar and India from Africa is dated 165–121 Mya (late Jurassic-early Cretaceous) (Vences et al., 2001; Chakrabarty, 2004). Fig. 26 shows the position of continental plates in Early Jurassic (195 Mya), just

before the fragmentation of Gondwanaland started. Judging from their geographical distribution, by this time all six groups of buthoid scorpions outlined in our phylogeny should have been already present in various fragments of Laurasia and Gondwanaland (compare with the discussion on historical biogeography of Hemiscorpiidae by Soleglad et al., 2005). The common ancestor of the genera belonging to the *Uroplectes* group, therefore, should have been present at least in the African portion of Gondwanaland prior to the Jurassic.

A clear synapomorphy of tibial spur loss separates nine genera in a Neotropical *Tityus* group. There can be no doubt that this group (i.e. all New World buthoid genera except *Ananteris* and *Microananteris*) is a derived lineage of buthoids. It should have been separated from its Afrotropical relatives (*Uroplectes* group) with the Western Gondwanaland fragmentation and formation of South America. By most recent estimates, the split of South America from Africa is dated 101–86 Mya (mid-Cretaceous) (Vences et al., 2001; Chakrabarty, 2004). The representatives of *Tityus* group could have reached North America already by the Tertiary and long before the Panama Isthmus formation, probably via the Caribbean stepping-stones (as evidenced by the Eocene *Uintascorpio*; Santiago-Blay et al., 2004b), and had ample time for producing an independent arid-adapted forms represented by the sole North American genus *Centruroides* (known from the Miocene). However, since the deserts of the New World are much younger, and also probably since most arid niches in North America were occupied by Vaejovidae and Caraboctonidae, and in South America, by Bothriuridae and Caraboctonidae, the Buthoidea in the New World never exhibited such radiation in the deserts as in the Old World.



**Figure 26:** Position of continental plates in early Jurassic period (195 Mya) (after Scotese, 2001, in part).

## Further discussion

Fet et al. (2003) presented the first pilot DNA phylogeny including 17 genera of Buthidae based on a small fragment of mitochondrial 16S rRNA gene. Of these, a well-supported monophyletic clade of 13 Palearctic *beta* genera falls completely within our *Buthus* group. On the other hand, four remaining genera (*Lychas*, *Groshus*, *Centruroides*, and *Rhopalurus*) formed a topology following that presented in this paper, with the Old World *Lychas* (*Ananteris* group) forming an outgroup to three remaining *alpha* genera. The well-supported monophyletic clade of *Groshus* (*Uroplectes* group) and *Centruroides* + *Rhopalurus* (*Tityus* group), revealed by this pilot DNA phylogeny, is in full agreement with the morphology-based phylogeny presented in our current paper. Further DNA sequence analysis of additional *Tityus* group genera (*Alayotityus*, *Microtityus*, *Tityus*; R. Teruel & V. Fet, in progress) confirms their grouping with the Madagascan *alpha* genus *Groshus* (*Uroplectes* group). These preliminary molecular data should be supplemented with much more DNA information in order to resolve deep monophyletic lineages.

A very interesting, if also partial, corroboration of buthoid relationships keeps coming from the data provided by toxicology research. For a long time it was known that "Old World" and "New World" Buthidae have pharmacologically different toxins. In fact, this knowledge derives almost exclusively from two groups of buthoids limited to a few highly toxic genera: in the Old World, these are *Androctonus*, *Buthus*, *Hottentotta*, *Leiurus*, *Mesobuthus*, and *Orthochirus*; and in the New World, *Centruroides* and *Tityus*. These two groups, in our phylogenetic scheme, appear at the extremes of buthoid phylogeny: the first one represents the  $d_3/DM_c$  *beta* genera (*Buthus* group) while *Centruroides* and *Tityus* belong to the *Tityus* group, i.e. the New World branch of  $DM_c/d_3$  *alpha* group (with their synapomorphic tibial spur loss).

Froy & Gurewitz (2003) published a phylogenetic tree for several classes of buthoid sodium channel toxins (*alpha*- and *beta*-toxins). They considered *beta*-like toxins ancestral, and suggested that in the Old World, they gave rise to mostly excitatory and depressant toxins; and in the New World, to a new, independent type of toxin group (*alpha*-prime toxins). An ancestral *beta*-toxin was also recently discovered in *Leiurus* (Gordon et al., 2003).

We can interpret the toxin information in the following way:

(a) excitatory and depressant toxins are clearly a synapomorphy of the Laurasian, arid-adapted *Buthus* group, including mammal-specific toxins, which probably evolved under Tertiary aridization and increased predation pressure from small mammals (Fet et al., 2003);

(b) modern *beta*-toxins are a synapomorphy of the New World *Tityus* group;

(c) so-called alpha-prime toxins, found only in *Centruroides*, are most likely a synapomorphy of this genus, which also belongs to the *Tityus* group.

It is important to note that, in the phylogeny of Froy & Gurewitz (2003), a so-called birtoxin, known from the Afrotropical genus *Parabuthus*, clusters with the *Tityus* group toxins. This would be expected from our independent morphology-based phylogeny since *Parabuthus* belongs to the *Uroplectes* group. The further toxin knowledge for the *Uroplectes* group as well as other groups of genera (first of all from the *Ananteris* and *Ismaginus* groups) could prove important in further understanding of buthoid phylogeny as well as the evolution of their toxins.

At this moment, we refrain from any nomenclatural endorsements in assigning taxonomic names to the groups of buthoid genera distinguished in this analysis. As demonstrated by Fet & Lowe (2000), most names historically offered for the subfamilies of Buthidae have never been formally synonymized and technically remain not only available but also valid. These names should be applied as soon as monophlyies in Buthoidea are clarified. Further ongoing research (Fet et al., in progress) addressing a multiple character set will possibly lead to a better understanding of phylogeny and systematics of Buthoidea.

## Acknowledgements

We thank Matt Braunwalder, Jonathan Coddington, Moira FitzPatrick, David Hirst, František Kovařík, Scott Larcher, Samuel D. Miller, Peter Schwedinger, W. David Sissom, Rolando Teruel and the Oman Natural History Museum for the loans and/or gifts of specimens. We thank Luis Acosta, Vanessa Dozeman, Elizabeth Fet, and Jan Ove Rein for their kind help.

## References

- ARMAS, L. F., DE. 1973. Escorpiones del Archipiélago Cubano. I. Nuevo género y nuevas especies de Buthidae (Arachnida, Scorpionida). *Poeyana*, 114: 1–23.
- ARMAS, L. F., DE. 1977. Redescripción de *Tityus obtusus* (Karsch 1879) (Scorpionida, Buthidae). *Poeyana*, 178: 1–7.
- ARMAS, L. F., DE. 1982. Adiciones a las escorpiofauñas (Arachnida: Scorpiones) de Puerto Rico y República Dominicana. *Poeyana*, 237: 1–25.
- ARMAS, L. F., DE. 1983. The Lesser Antillean scorpions of the genus *Centruroides*. *Uitgaven “Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen”*, Utrecht, 15(197), 11: 55–67.

ARMAS, L. F., DE. 1984. Escorpiones del Archipiélago Cubano. 7. Adiciones y enmiendas (Scorpiones: Buthidae, Diplocentridae). *Poeyana*, 275: 1–37.

ARMAS, L. F., DE. 1996. Presencia de *Centruroides schmidti* Sissom en el sureste de México y descripción de dos especies nuevas (Scorpiones: Buthidae). *Revista Nicaraguana de Entomología*, 36: 21–33.

ARMAS, L. F., DE. 1999. Quince nuevos alacranes de La Española y Navassa, Antillas Mayores (Arachnida: Scorpiones). *Avicennia*, 10/11: 101–136.

ARMAS, L. F., DE & E. MARTÍN FRÍAS. 1998. Presencia del género *Tityopsis* en México y descripción de una especie nueva (Scorpiones: Buthidae). *Anales de la Escuela nacional de Ciencias biológicas*, México, 43: 45–49.

(BIRULA, A. A.) BYALYNITSKII-BIRULYA, A. A. 1917a. Arachnoidea Arthrogaster Caucasicus. Pars I. Scorpiones. *Zapiski Kavkazskogo Muzeya (Mémoires du Musée du Caucase)*, Tiflis: Imprimerie de la Chancellerie du Comité pour la Transcaucasie, A(5), 253 pp. (in Russian; published August 1917). English translation: Byalynitskii-Birulya, A. A. 1964. *Arthrogastriac Arachnids of Caucasia*. 1. Scorpions. Jerusalem: Israel Program for Scientific Translations, 170 pp.

(BIRULA, A. A.) BYALYNITSKI-BIRULYA, A. A. 1917b. *Faune de la Russie et des pays limitrophes fondee principalement sur les collections du Musée Zoologique de l'Académie des Sciences de Russie. Arachnides (Arachnoidea)*. Petrograd, 1(1): xx, 227 pp. (in Russian; Introduction dated October 1917). English translation: Byalynitskii-Birulya, A. A. 1965. *Fauna of Russia and Adjacent Countries. Arachnoidea. Vol. I. Scorpions*. Jerusalem: Israel Program for Scientific Translations, xix, 154 pp.

CAPES, E. M. & V. FET. 2001. A redescription of the scorpion genus *Plesiobuthus* Pocock, 1900 (Scorpiones: Buthidae) from Pakistan. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13(164): 295–304.

CHAKRABARTY, P. 2004. Cichlid biogeography: comment and review. *Fish and Fisheries*, 5: 97–119.

CODDINGTON, J. A., G. GIRIBET, M. S. HARVEY, L. PRENDINI & D. E. WALTER. 2004. Arachnida. Pp. 296–318 in Cracraft, J. & M. J. Donoghue (eds.). *Assembling the Tree of Life*. New York, NY: Oxford University Press.

FET, V. 1987. [A new genus and species of a scorpion from East Karakum: *Pectinibuthus birulai* Fet n.g. n.sp. (Scorpiones, Buthidae)]. *Entomologicheskoe Obozrenie (Revue d'Entomologie de l'URSS)*, 66(2): 443–446.

FET, V. 2000. Family Microcharmidae. Pp. 412–423 in Fet, V., W. D. Sissom, G. Lowe & M. E. Braunwalder. *Catalog of the Scorpions of the World (1758–1998)*. 690 pp. New York: New York Entomological Society.

FET, V., E. M. CAPES & W. D. SISSOM. 2001. A new genus and species of psammophilic scorpion from eastern Iran (Scorpiones, Buthidae). Pp 183–189 in Fet, V. & P. A. Selden (eds.). *Scorpions 2001. In memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society.

FET, V., B. GANTENBEIN, A. V. GROMOV, G. LOWE & W. R. LOURENÇO. 2003. The first molecular phylogeny of Buthidae (Scorpiones). *Euscorpius*, 4: 1–10.

FET, V. & G. LOWE. 2000. Family Buthidae. Pp. 54–286 in Fet, V., W. D. Sissom, G. Lowe & M. E. Braunwalder. *Catalog of the Scorpions of the World (1758–1998)*. 690 pp. New York: New York Entomological Society.

FET, V., G. A. POLIS & W. D. SISSOM. 1998. Life in sandy deserts: the scorpion model. *Journal of the Arid Environments*, 39: 609–622.

FET, V., M. E. SOLEGLAD & A. V. GROMOV. 2004. The platypus of a scorpion: genus *Pseudochactas* (Scorpiones: Pseudochactidae). *Proceedings of the 3d Scorpiology Symposium, American Arachnological Society 28<sup>th</sup> Annual Meeting*, Norman, Oklahoma, 28 June 2004. *Euscorpius*, 17: 61–68.

FRANCKE, O. F. & W. D. SISSOM. 1980. Scorpions from the Virgin Islands (Arachnida, Scorpiones). *Occasional Papers of the Museum, Texas Tech University*, 65: 1–19.

FRANCKE, O. F. & S. A. STOCKWELL. 1987. Scorpions (Arachnida) from Costa Rica. *Special Publications of The Museum, Texas Tech University*, 25: 1–64.

FROY, O. & M. GUREVITZ. 2003. New insight on scorpion divergence inferred from comparative analysis of toxin structure, pharmacology and distribution. *Toxicon*, 42(5): 549–555.

GONZÁLEZ-SPONGA, M. A. 1981. Un nuevo género y dos nuevas especies de la familia Buthidae de Venezuela (Arachnida, Escorpiones). *Monografías Científicas "Augusto Pi Suñer"* (Caracas, Instituto Pedagógico), 13: 1–30.

GONZÁLEZ-SPONGA, M. A. 1996a. Arácnidos de Venezuela: seis nuevas especies del género *Tityus* y redescrición de *Tityus pococki* Hirst, 1911, *Tityus rugosus* (Scenkel, 1932) n. comb. y *Tityus nematochirus* Mello-Leitão, 1940 (Scorpionida: Buthidae). *Acta Biológica Venezolana*, 16(3): 1–38.

GONZÁLEZ-SPONGA, M. A. 1996b. *Guía para identificar escorpiones de Venezuela*. Caracas: Cuadernos Lagoven, 204 pp.

GORDON, D., N. ILAN, N. ZILBERBERG, N. GILLES, D. URBACH & L. COHEN. 2003. An 'Old World' scorpion β-toxin that recognizes both insect and mammalian sodium channels. A possible link towards diversification of β-toxins. *European Journal of Biochemistry*, 270: 2663–2670.

JERAM, A. J. 1994a. Carboniferous Orthosterni and their relationship to living scorpions. *Palaeontology*, 37(3): 513–550.

JERAM, A. J. 1994b. Scorpions from the Viséan of East Kirkton, West Lothian, Scotland, with a revision of the infraorder Mesoscorpionina. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 84: 283–299.

KITCHING, I. J., P. L. FOREY, C. J. HUMPHRIES & D. WILLIAMS. 1998. *Cladistics – Theory and Practice of Parsimony Analysis*. 2<sup>nd</sup> ed. London: Oxford University Press, 242 pp.

KOVAŘÍK, F. 1994. *Isometrus zideki* sp. n. from Malaysia and Indonesia, and a taxonomic position of *Isometrus formosus*, *I. thurstoni* and *I. sankariensis* (Arachnida: Scorpionida: Buthidae). *Acta Societas Zoologicae Bohemicae*, 58: 195–203.

KOVAŘÍK, F. 1995. Review of Scorpionida from Thailand with descriptions of *Thaicharmus mahunkai* gen. et sp. n. and *Lychas krali* sp. n. (Buthidae). *Acta Societas Zoologicae Bohemicae*, 59: 187–207.

KOVAŘÍK, F. 1996. *Baloorthochirus becvari* gen. et sp. n. from Pakistan, and taxonomic position of *Orthochirus luteipes* (Scorpionida: Buthidae). *Acta Societas Zoologicae Bohemicae*, 60: 177–181.

KOVAŘÍK, F. 1997a. *Afroisometrus* gen. n. from Zimbabwe (Scorpiones: Buthidae). *Acta Societas Zoologicae Bohemicae*, 61: 35–37.

KOVAŘÍK, F. 1997b. Results of the Czech Biological Expedition to Iran. Part 2. Arachnida: Scorpiones with descriptions of *Iranobuthus krali* gen. n. et sp. n. and *Hottentotta zagrosensis* sp. n. (Buthidae). *Acta Societas Zoologicae Bohemicae*, 61: 39–52.

KOVAŘÍK, F. 1997c. Revision of the genera *Lychas* and *Hemilychas*, with descriptions of six new species (Scorpiones: Buthidae). *Acta Societas Zoologicae Bohemicae*, 61: 311–371.

KOVAŘÍK, F. 1997d. *Isometrus kurkai* sp. n. from Indonesia (Scorpiones, Buthidae). *Časopis Národního Muzea, Řada Přírodovědná*, 166(1–4): 5–10.

KOVAŘÍK, F. 1998. Three new genera and species of Scorpiones (Buthidae) from Somalia. *Acta Societas Zoologicae Bohemicae*, 62: 115–124.

KOVAŘÍK, F. 2001. *Lanzatus somalicus* gen. et sp. n. (Scorpiones: Buthidae) from Somalia. *Acta Societas Zoologicae Bohemicae*, 65: 41–44.

KOVAŘÍK, F. 2004. Revision and taxonomic position of genera *Afghanorthochirus* Lourenço & Vachon, *Baloorthochirus* Kovařík, *Butheolus* Simon, *Nanobuthus* Pocock, *Orthochiroides* Kovařík, *Pakistanorthochirus* Lourenço, and Asian *Orthochirus* Karsch, with descriptions of twelve new species (Scorpiones, Buthidae). *Euscorpius*, 16: 1–33.

KRAEPELIN, K. 1899. Scorpiones und Pedipalpi. In F. Dahl (ed.), *Das Tierreich. Herausgegeben von der Deutschen Zoologischen Gesellschaft*. Berlin: R. Friedländer und Sohn Verlag, 8 (Arachnoidea): 1–265.

KRAEPELIN, K. 1905. Die geographische Verbreitung der Skorpione. *Zoologische Jahrbücher, Abtheilung für Systematik*, 22(3): 321–364.

LAMORAL, B. H. 1976. *Akentrobuthus leleupi*, a new genus and species of humicolous scorpion from eastern Zaire, representing a new subfamily of the Buthidae. *Annals of the Natal Museum*, 22(3): 681–691.

LEVY, G. & P. AMITAI. 1980. *Fauna Palaestina. Arachnida I. Scorpiones*. Jerusalem: The Israel Academy of Sciences and Humanities, 130 pp.

LEVY, G., P. AMITAI & A. SHULOV. 1973. New scorpions from Israel, Jordan and Arabia. *Zoological Journal of the Linnaean Society*, 52(2): 113–140.

LOCKET, N. A. 1990. A new genus and species of scorpion from South Australia (Australia) (Buthidae: Buthinae). *Transactions of the Royal Society of South Australia*, 114(2): 67–80.

LOURENÇO, W. R. 1980a. Compléments à la description de *Tityus kraepelini* Borelli, 1899 (Scorpiones, Buthidae). *Bollettino dei Museo di Zoologia dell'Università di Torino*, (1980) 6: 61–68.

LOURENÇO, W. R. 1980b. Contribution à la connaissance systématique des Scorpions appartenant au 'complexe' *Tityus trivittatus* Kraepelin, 1898 (Buthidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, 2(3): 793–843.

LOURENÇO, W. R. 1981. Scorpions cavernicoles de l'Équateur: *Tityus demangei* n. sp. et *Ananteris ashmolei* n. sp. (Buthidae); *Troglotayosicus vachoni* n. gen. n. sp. (Chactidae), Scorpion troglobie. *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, 3(2): 635–662.

LOURENÇO, W. R. 1982a. *Tityus gasci*, nouvelle espèce de Scorpion Buthidae de Guyane française. *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, 3(3): 841–845 (date on cover 1981; published 15 February 1982).

LOURENÇO, W. R. 1982b. Révision du genre *Ananteris* Thorell, 1891 (Scorpiones, Buthidae) et description de six espèces nouvelles. *Bulletin du Muséum National d'Histoire Naturelle, Paris, (Zoologie, Biologie et Écologie Animale)*, 4(1–2): 119–151.

LOURENÇO, W. R. 1982c. Contribuição ao conhecimento sistemático e biológico de *Tityus pusillus* Pocock, 1893 (Scorpiones, Buthidae). *Revista Nordestina da Biologia*, 5(1): 35–43.

LOURENÇO, W. R. 1982d. La véritable identité de *Tityus bahiensis* (Perty, 1834). Description de *Tityus eickstedtiae* n. sp. (Scorpiones, Buthidae). *Revue Arachnologique*, 3(4): 93–105.

LOURENÇO, W. R. 1983a. La faune des Scorpions de Guyane Francaise. *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, 5(3): 771–808.

LOURENÇO, W. R. 1983b. Étude d'une petite collection de Scorpions du Nicaragua, avec la description d'une espèce nouvelle de *Centruroides* (Buthidae). *Revue Suisse de Zoologie*, 90(3): 761–768.

LOURENÇO, W. R. 1983c. Resultados faunísticos de diversas campañas realizadas en América Latina. IV. Estudo de uma pequena coleção de escorpiões do Perú e Equador, com a redescricao de *Tityus ecuadorensis* Kraepelin, 1896. *Speleon*, 26: 11–15.

LOURENÇO, W. R. 1983d. Contribution à la connaissance du Scorpion amazonien *Tityus metuendus* Pocock, 1897 (Buthidae). *Studies on Neotropical Fauna and Environment*, 18(4): 185–193.

LOURENÇO, W. R. 1984a. Étude systématique de quelques espèces appartenant au complexe *Tityus forcipula* (Gervais, 1844) (Scorpiones, Buthidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, 6(3): 729–739.

LOURENÇO, W. R. 1984b. Contribution à la connaissance de *Centruroides barbusensis* (Pocock, 1898) (Scorpiones, Buthidae). *Journal of Arachnology*, 11(3) (1983): 327–335.

LOURENÇO, W. R. 1984c. *Ananteris luciae*, nouvelle espèce de Scorpion de l'Amazonie brésilienne (Scorpiones, Buthidae). *Journal of Arachnology*, 12(3): 279–282.

LOURENÇO, W. R. 1984d. Notas taxonomicas sobre *Tityus trinitatis* Pocock, 1897 (Scorpiones, Buthidae). *Revista Brasileira da Biologia*, 44(1): 15–19.

LOURENÇO, W. R. 1984e. Considérations sur les espèces de *Tityus* (Scorpiones, Buthidae) décrites des Petites Antilles. *Revue Arachnologique*, 5(3): 91–105.

LOURENÇO, W. R. 1985. Le véritable statut des genres *Ananteris* Thorell, 1891 et *Ananteroides* Borelli, 1911 (Scorpiones: Buthidae). *Annals of the Natal Museum*, 1985: 407–416.

LOURENÇO, W. R. 1986a. Les Scorpions de la station écologique de Lamto (Côte d'Ivoire). *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, 8(1): 199–208.

LOURENÇO, W. R. 1986b. *Tityus cerroazul*, nouvelle espèce de Scorpion de Panama (Scorpiones, Buthidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, 8(3): 637–641.

LOURENÇO, W. R. 1987. Considerações sistemáticas sobre *Tityus magnimanus* Pocock, 1897 (Scorpiones, Buthidae) e espécies associadas. *Revista Brasileira da Biologia*, 47(4): 565–572.

LOURENÇO, W. R. 1992. Biogéographie des espèces du groupe naturel «*Tityus clathratus*» (Chelicerata, Scorpiones, Buthidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, (4), 14(2): 473–481.

LOURENÇO, W. R. 1995a. Considérations sur la répartition géographique du genre *Butheoloides* Hirst avec la description de *Butheoloides wilsoni* nov. sp. (Scorpiones, Buthidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, (4), (1994), 16A(2–4): 475–480.

LOURENÇO, W. R. 1995b. Description de trois nouveaux genres et quatre nouvelles espèces de scorpions Buthidae de Madagascar. *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, (4), 17A(1–2): 95–106.

LOURENÇO, W. R. 1995c. The remarkable discovery of a new and extinct species of *Tityus* from Martinique in Lesser Antilles (Chelicerata, Scorpiones, Buthidae). *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Ser. Zool.*, 66(1): 27–32.

LOURENÇO, W. R. 1996a. *Faune de Madagascar. 87. Scorpions (Chelicerata, Scorpiones)*. Paris: Muséum National d'Histoire Naturelle, 102 pp.

LOURENÇO, W. R. 1996b. A propos de deux espèces nouvelles appartenant au genre *Butheoloides* Hirst (Scorpiones, Buthidae). *Revue Arachnologique*, 11(9): 87–94.

LOURENÇO, W. R. 1996c. *Microcharmus hauseri*, nouvelle espèce de Scorpion de Madagascar (Scorpiones, Buthidae). *Revue Suisse de Zoologie*, 103(2): 319–322.

LOURENÇO, W. R. 1996d. A new genus and a new species of scorpion (Buthidae) from Iran. *Zoology in the Middle East*, 12: 93–98.

LOURENÇO, W. R. 1997a. Finding lost diversity in old collections: *Tityus anneae*, a new species of scorpion from Brazil found in the old Simon collection deposited in the Natural History Museum, Paris. *Biogeographica*, 73(3): 135–140.

LOURENÇO, W. R. 1997b. Another new species of *Tityobuthus* from Madagascar (Scorpiones, Buthidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 12(155): 147–151.

LOURENÇO, W. R. 1997c. A propos de deux nouvelles espèces de *Tityus* Koch du Brésil (Scorpiones, Buthidae). *Revue Arachnologique*, 12(5): 53–59.

LOURENÇO, W. R. 1997d. Synopsis de la faune de scorpions de Colombie, avec des considérations sur la systématique et la biogéographie des espèces. *Revue suisse de Zoologie*, 104(1): 61–94.

LOURENÇO, W. R. 1997e. Additions à la faune de scorpions néotropicaux. *Revue suisse de Zoologie*, 104(3): 587–604.

LOURENÇO, W. R. 1997f. A new species of *Lychas* Koch, 1845 (Chelicerata, Scorpiones, Buthidae) from Sri Lanka. *Revue suisse de Zoologie*, 104(4): 831–836.

LOURENÇO, W. R. 1998a. Une nouvelle famille est nécessaire pour des microscorpions humicoles de Madagascar et d'Afrique. *Comptes Rendus des Séances de l'Académie des Sciences, Paris, Ser. Sci. Vie*, 321: 845–848.

LOURENÇO, W. R. 1998b. A new species of *Apistobuthus* Finnegan, 1932 (Scorpiones, Buthidae) from Iran. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 12(157): 237–244.

LOURENÇO, W. R. 1998c. *Uroplectoides abyssinicus* gen. n., sp. n., a new genus and new species of scorpion (Scorpiones, Buthidae) from Ethiopia. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 12(158): 309–316.

LOURENÇO, W. R. 1998d. A new species of *Tityus* C. L. Koch, 1836 (Scorpiones, Buthidae) in Colombia, with a check list and key to the Colombian species of the genus. *Zoosystema*, 20(3): 487–497.

LOURENÇO, W. R. 1999a. New species of *Ananteris* from the north of Chocó, Colombia (Scorpiones: Buthidae). *Anales del Instituto de Biología Universidad Nacional Autónoma de México, Serie Zoológica* 70(2): 93–98. *leilae*

LOURENÇO, W. R. 1999b. Origines et affinités des scorpions des Grandes Antilles: le cas particulier des éléments de la famille des Buthidae. *Bio-geographica* (Paris), 75(3): 131–144.

LOURENÇO, W. R. 1999c. Biogeography, biodiversity and old collections: a new genus and species of buthid scorpion from Congo found in the collections of the Muséum National d'Histoire Naturelle, Paris. *Biogeographica*, 75(4): 187–192.

LOURENÇO, W. R. 1999d. A new species of *Cicileus* Vachon, 1948 (Chelicerata, Scorpiones, Buthidae) from Niger. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13(159): 29–36.

LOURENÇO, W. R. 1999e. Two new species of *Comp-sobuthus* Vachon (Scorpiones, Buthidae) from Africa. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13(160): 85–94.

LOURENÇO, W. R. 1999f. Some remarks about *Ananteris festae* Borelli, 1899 and description of a new species of *Ananteris* Thorell from Ecuador (Scorpiones, Buthidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13(160): 95–100.

LOURENÇO, W. R. 1999g. Notes on the scorpions collected during the Fuhrmann's expedition to Colombia and described by Kraepelin. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13(161): 123–132.

LOURENÇO, W. R. 1999h. A new species of *Grosphus* Simon (Scorpiones, Buthidae), the first record of an intertidal scorpion from Madagascar. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13(161): 133–138.

LOURENÇO, W. R. 1999i. A new species of *Tityus* Koch, 1836 (Chelicerata, Scorpiones, Buthidae) from Department Cesar in Colombia. *Revue Arachnologique*, 13(1): 1–6.

LOURENÇO, W. R. 1999j. Complementary notes on the phylogenetic position of the genus *Lychasioides* Vachon, 1973, and redescription of *Lychasioides amieti* (Chelicerata, Scorpiones, Buthidae). *Revue Arachnologique*, 13(1): 7–13.

LOURENÇO, W. R. 1999k. Un nouveau genre et une nouvelle espèce de scorpion d'Egypte, appartenant à la famille des Buthidae Simon. *Revue suisse de Zoologie*, 106(3): 591–598.

LOURENÇO, W. R. 2000a. Un nouveau genre de Scorpion malgache, maillon possible entre les Micro-charmidae et les Buthidae. *Comptes Rendus de l'Académie des Sciences Paris, Sciences de la vie*, 323: 877–881.

LOURENÇO, W. R. 2000b. The genus *Hottentotta* Birula 1908, with the description of a new subgenus and species from India (Scorpiones, Buthidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13 (162): 191–195.

LOURENÇO, W. R. 2000c. A new species of *Buthacus* Birula (Scorpiones, Buthidae) from Morocco. *Faunistische Abhandlungen, Staatliches Museum Tierkunde, Dresden*, 30, 22(1): 5–9.

LOURENÇO, W. R. 2000d. Synopsis of the Colombian species of *Tityus* Koch (Chelicerata, Scorpiones, Buthidae), with descriptions of three new species. *Journal of Natural History*, 34: 449–461.

LOURENÇO, W. R. 2000e. Taxonomic considerations about the genus *Charmus* Karsch, 1879 (Chelicerata, Scorpiones, Buthidae) with description of a new species to India. *Memorie della Società Entomologica Italiana*, 78(2): 295–303.

LOURENÇO W. R. 2000f. Confirmation d'une espèce nouvelle appartenant au genre *Butheoloides* Hirst (Scorpiones, Buthidae) du Nigéria. *Revue Arachnologique*, 13 (9): 129–133.

LOURENÇO, W. R. 2000g. More about the Buthoidea of Madagascar, with special references to the genus *Tityobuthus* Pocock (Scorpiones, Buthidae). *Revue suisse de Zoologie*, 107(4): 721–736.

LOURENÇO, W. R. 2000h. Analyse taxonomique de quelques espèces du genre *Uroplectes* Peters, 1861 présentes en Angola et description d'une espèce nouvelle (Scorpiones, Buthidae). *Zoosystema*, 22(3): 499–506.

LOURENÇO, W. R. 2001a. Un nouveau genre de Buthidae, probable vicariant géographique d'*Anomalobuthus* Kraepelin (Chelicerata, Scorpiones). *Bio-geographica*, 77(1): 15–20.

LOURENÇO, W. R. 2001b. A remarkable scorpion fossil from the amber of Lebanon. Implication for the phylogeny of Buthoidea. *Comptes Rendus de l'Académie des Sciences Paris*, 332: 641–646.

LOURENÇO, W. R. 2001c. Further taxonomic consideration on the Northwestern African species of

*Buthacus* Birula (Scorpiones, Buthidae), and description of two new species. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13 (163): 255–269.

LOURENÇO, W. R. 2001d. A new species of *Compsobuthus* Vachon, 1949 from Afghanistan (Scorpiones, Buthidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13(164): 315–319.

LOURENÇO, W. R. 2001e. The Brazilian scorpion *Tityus stigmurus* (Chelicerata, Buthidae) and its complex of morphos. A new model is needed. *Bio-geographica*, 77(1): 21–34.

LOURENÇO, W. R. 2001f. Un nouveau genre et une nouvelle espèce de scorpion d'Algérie, avec des considérations taxonomiques sur le genre *Lissothus* Vachon, 1948 (Scorpiones, Buthidae). *Zoosystema*, 23(1): 51–57.

LOURENÇO, W. R. 2001g. Description of a new species of *Ananteris* Thorell, 1891 from the south of French Guyana (Scorpiones, Buthidae). *Zoosystema*, 23(4): 689–693.

LOURENÇO, W. R. 2001h. Taxonomic considerations on the genera *Butheolus* Simon, *Nanobuthus* Pocock and *Neobuthus* Hirst (Scorpiones, Buthidae) with the description of a new species of *Neobuthus* from Ethiopia. Pp. 171–183 in Prakash, I. (ed.), *Ecology of Desert Environments. (A Festschrift for Prof. J. L. Cloudsley-Thompson on his 80<sup>th</sup> Birthday)*. Jodhpur: Scientific Publishers.

LOURENÇO, W. R. 2001i. Sur les pas de Jean A. Vellar. A propos de sa contribution à l'étude des scorpions (Chelicerata). *Revista Ibérica de Aracnología*, 3: 25–36.

LOURENÇO, W. R. 2001j. Another new species of *Grosphus* Simon (Scorpiones, Buthidae) for Madagascar. *Revue suisse de Zoologie*, 108(3): 455–461.

LOURENÇO, W. R. 2002a. Nouvelles considérations sur la classification et la biogéographie du genre *Microbuthus* Kraepelin (Scorpions, Buthidae): caractérisation d'une nouvelle sous-espèce pour le Maroc. *Biogeographica*, 78(4): 165–176.

LOURENÇO, W. R. 2002b. Notes on the taxonomy and geographical distribution of *Buthiscus bicalcaratus* Birula, 1905 (Scorpiones, Buthidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 14(165): 11–16.

LOURENÇO, W. R. 2002c. Further taxonomic considerations about the genus *Charmus* Karsch, 1879 (Scorpiones, Buthidae), with the description of a new species from Sri Lanka. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 14(165): 17–25.

LOURENÇO, W. R. 2002d. Nouvelles additions à la faune de scorpions néotropicaux (Scorpiones, Buthidae). *Revue suisse de Zoologie*, 109(1): 127–141.

LOURENÇO, W. R. 2002e. Nouvelles considérations sur la systématique et la biogéographie du genre *Butheoloides* Hirst (Scorpiones, Buthidae) avec description d'un nouveau sous-genre et de deux nouvelles espèces. *Revue suisse de Zoologie*, 109(4): 725–733.

LOURENÇO, W. R. 2003a. Humicolous buthoid scorpions: a new genus and species from French Guiana. *Comptes Rendus Biologies*, 326(12): 1149–1155.

LOURENÇO, W. R. 2003b. Notes on *Isometroides vescus* (Karsch, 1880) (Scorpiones, Buthidae), an endemic element to Australia. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 14(167): 105–110.

LOURENÇO, W. R. 2003c. Description of a new species of *Tityus* (Scorpiones, Buthidae) from Serra da Jurema in the State of Bahia, Brazil. *Revista Ibérica de Aracnología*, 7: 109–115.

LOURENÇO, W. R. 2003d. The genus *Ananteris* Thorell (Scorpiones, Buthidae) in French Guyana. *Revista Ibérica de Aracnología*, 7: 183–188.

LOURENÇO, W. R. 2003e. Description of a new species of scorpion belonging to the genus *Himalayotityobuthus* Lourenço (Scorpiones, Buthidae). *Revista Ibérica de Aracnología*, 7: 225–229.

LOURENÇO, W. R. 2003f. New taxonomic considerations on some species of the genus *Grosphus* Simon, with description of a new species (Scorpiones, Buthidae). *Revue suisse de Zoologie*, 110(1): 141–154.

LOURENÇO, W. R. 2003g. Description of a new species of *Tityus* (Scorpiones, Buthidae) from Serra do Cipo in the State of Minas Gerais, Brazil. *Revue suisse de Zoologie*, 110(2): 427–435.

LOURENÇO, W. R. 2004a. Humicolous microcharmid scorpions: a new genus and species from Madagascar. *Comptes Rendus Biologies*, 327(1): 77–83.

LOURENÇO W. R. 2004b. On the genus *Hottentotta* Birula 1908, with the description of a new species from Chad (Scorpiones: Buthidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 14(170): 211–218.

LOURENÇO W. R. 2004c. Description of a new species of *Buthacus* Birula, 1908 (Scorpiones, Buthidae) from Afghanistan. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 14(170): 205–210.

LOURENÇO, W. R. 2004d. A new species of *Compso-buthus* Vachon, 1949 from India (Scorpiones, Buthidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 14(169): 157–163.

LOURENÇO W. R. 2004e. The genus *Ananteris* Thorell (Scorpiones, Buthidae) in the Brazilian Amazonia. *Revista Ibérica de Aracnología*, 9: 137–140.

LOURENÇO W. R. 2004f. List of the species of *Ananteris* Thorell, 1891 (Scorpiones, Buthidae) with a description of a new species from the state of Bahia, Brazil. *Revista Ibérica de Aracnología*, 10: 163–166.

LOURENÇO, W. R. 2004g. New considerations on the Northwestern African species of *Buthacus* Birula (Scorpiones, Buthidae), and description of a new species. *Revista Ibérica de Aracnología*, 10: 225–231.

LOURENÇO, W. R. 2004h. Further considerations regarding *Tityobuthus baroni* (Pocock, 1890) with the description of a new species from Ste Marie Island, Madagascar (Scorpiones, Buthidae). *Zoosystema*, 26(3): 385–392.

LOURENÇO W. R. 2004i. Scorpions du Sud-ouest de Madagascar et en particulier de la forêt de Mikea. Pp. 25–35 in Raselimanana, A.P. & S. M. Goodman (eds). *Inventaire floristique et faunistique de la forêt de Mikea: Paysage écologique et diversité biologique d'une préoccupation majeure pour la conservation*. Série Sciences Biologiques, 21, Antananarivo, Madagascar.

LOURENÇO W. R. 2005a. Description of three new species of scorpion from Sudan (Scorpiones, Buthidae). *Boletín Sociedad Entomológica Aragonesa*, 36: 21–28.

LOURENÇO, W. R. 2005b. Nouvelles considérations taxonomiques sur les espèces du genre *Androctonus* Ehrenberg, 1828 et description de deux nouvelles espèces (Scorpiones, Buthidae). *Revue suisse de Zoologie*, 112 (1): 145–171.

LOURENÇO, W. R., R. L. G. BAPTISTA & A. P. DE LEÃO GIUPPONI. 2004a. Troglobitic scorpions: a new genus and species from Brazil. *Comptes Rendus Biologies*, 327(12): 1151–1156.

LOURENÇO, W. R. & O. F. FRANCKE. 1984. The identities of *Tityus floridanus* and *Tityus tenuimanus* (Scorpiones, Buthidae). *Florida Entomologist*, 67(3): 424–429.

LOURENÇO W. R. & D. HUBER. 1999a. One more new species of *Lychas* Koch, 1845 (Chelicerata, Scorpiones, Buthidae) from Sri Lanka. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 13 (159): 23–27.

LOURENÇO W. R. & D. HUBER. 1999b. Additions to the scorpion faunas of Trinidad and Tobago. *Revue Suisse de Zoologie*, 106(1): 249–267.

LOURENÇO, W. R. & D. HUBER. 2000. Two new species of scorpions (Scorpiones, Buthidae) of the genus *Paraorthochirus* Lourenço & Vachon from Oman. *Zoology in the Middle East*, 20: 137–144.

LOURENÇO, W. R. & D. HUBER. 2002. New addition to the scorpion fauna (Arachnida: Scorpiones) of Sri Lanka. *Revue Suisse de Zoologie*, 109(2): 265–275.

LOURENÇO, W. R. & P. GENIEZ. 2005. A new scorpion species of the genus *Buthus* Leach, 1815 (Scorpiones, Buthidae) from Morocco. *Euscorpius*, 19: 1–6.

LOURENÇO, W. R. & S. M. GOODMAN. 1999. Taxonomic and ecological observations on the scorpions collected in the Forest of Ankazomivady–Ambositra and on the “RS d’Ivohibe”, Madagascar. *Revista de Biología Tropical*, 47(3): 475–482.

LOURENÇO, W. R. & S. M. GOODMAN. 2002. Scorpions from the Daraina region of northeastern Madagascar, with special reference to the family Heteroscorpionidae Kraepelin, 1905. *Revista Ibérica de Aracnología*, 6: 53–68.

LOURENÇO, W. R. & S. M. GOODMAN. 2003a. New considerations on the genus *Tityobuthus* Pocock (Scorpiones, Buthidae) and description of a new

species from the Ankarana in northern Madagascar. *Revista Ibérica de Aracnología*, 8: 13–22.

LOURENÇO, W. R. & S. M. GOODMAN. 2003b. Description of a new species of *Grosphus* Simon (Scorpiones, Buthidae) from the Ankarana Massif, Madagascar. *Revista Ibérica de Aracnología*, 8: 19–28.

LOURENÇO, W. R. & S. M. GOODMAN. 2004. A new species of *Tityobuthus* (Pocock) from Namoroka in the Province of Mahajanga, Madagascar (Scorpiones, Buthidae). *Revista Ibérica de Aracnología*, 9: 19–22.

LOURENÇO, W. R., S. M. GOODMAN & O. RAMILIAONA. 2004b. Three new species of *Grosphus* Simon from Madagascar (Scorpiones, Buthidae). *Revista Ibérica de Aracnología*, 9: 225–234.

LOURENÇO, W. R., M. B. KNOX & E. D. MAGALHÃES. 1997. Redescription of *Tityus blaseri* (Scorpiones: Buthidae) from Goias, Brazil. *Revista de Biología Tropical*, 45(4): 1579–1582.

LOURENÇO, W. R. & A. P. DE LEÃO GIUPPONI. 2004. Description of a new species of *Tityus* Koch, 1836 (Scorpiones, Buthidae) from the states of Espírito Santo and Rio de Janeiro in Brazil. *Revista Ibérica de Aracnología*, 10: 237–243.

LOURENÇO, W. R. & E. MÉNDEZ. 1984. Inventario preliminar sobre la fauna de escorpiones de Panamá, con algunas consideraciones taxonómicas y biogeográficas. *Revista de Biología Tropical*, 32(1): 85–93.

LOURENÇO, W. R., D. MODRY & Z. AMR. 2002. Description of a new species of *Leiurus* Ehrenberg, 1828 (Scorpiones, Buthidae) from the South of Jordan. *Revue suisse de Zoologie*, 109 (3): 635–642.

LOURENCO, W. R. & L. MONOD. 1998. Redescription of *Compsobuthus rugosulus* (Pocock, 1900) (Scorpiones, Buthidae), based on specimens of Pakistan. *Revue suisse de Zoologie*, 105(4): 789–796.

LOURENÇO, W. R. & R. OTERO PATIÑO. 1998. *Tityus antioquensis* sp.n., a new species of scorpion from the Department Antioquia, Central Cordillera of Colombia (Scorpiones, Buthidae), with a checklist and key for the Colombian species of the genus. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 12(158): 297–307.

LOURENÇO, W. R. & A. PÉZIER. 2002a. Addition to the scorpion fauna of the Manaus region (Brazil), with a description of two new species of *Tityus* from the canopy. *Amazoniana*, 17(1): 177–186.

LOURENÇO, W. R. & A. PÉZIER. 2002b. Taxonomic consideration of the genus *Odontobuthus* Vachon (Scorpiones, Buthidae), with description of a new species. *Revue suisse de Zoologie*, 109 (1): 115–125.

LOURENÇO, W. R., J.-X. QI & M.-S. ZHU. 2005a. Description of a new species of *Isometrus* Ehrenberg 1828 (Scorpiones, Buthidae) from the island of Hainan, China. *Boletín Sociedad Entomológica Aragonesa*, 36: 57–63.

LOURENÇO, W. R., J.-X. QI & M.-S. ZHU. 2005b. Description of two new species of scorpions from China (Tibet) belonging to the genera *Mesobuthus* Vachon (Buthidae) and *Heterometrus* Ehrenberg (Scorpionidae). *Zootaxa*, 985: 1–16.

LOURENÇO, W. R. & E. C. B. RAMOS. 2004. New considerations on the status of *Tityus magnimanus* Pocock, 1897 (Scorpiones: Buthidae), and a description of a new species of *Tityus* from the state of Roraima, Brazil. *Revista Ibérica de Aracnología*, 10: 285–291.

LOURENÇO, W. R. & T. SLIMANI. 2004. Description of a new scorpion species of the genus *Buthus* Leach, 1815 (Scorpiones: Buthidae) from Morocco. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 14(169): 165–170.

LOURENÇO, W. R., T. SLIMANI & A. BERAHOU. 2003. Le genre *Butheoloides* Hirst (Scorpiones, Buthidae); description d'une nouvelle espèce pour le Maroc avec des considérations écologiques et biogéographiques. *Biogeographica*, 70(1): 19–30.

LOURENÇO, W. R. & M. VACHON. 1995. Un nouveau genre et deux nouvelles espèces de scorpions Buthidae d'Iran. *Bulletin du Muséum National d'Histoire Naturelle, Paris (Zoologie, Biologie et Écologie Animale)*, (4), 17, A, (3–4): 297–305.

LOURENÇO, W. R. & M. VACHON. 1996. Compléments à la phylogénie et à la biogéographie des genres *Alayotityus* Armas et *Tityopsis* Armas (Scorpiones, Buthidae). *Biogeographica*, 72(1): 33–39.

LOURENÇO, W. R. & M. VACHON. 2001. A new species of *Compsobuthus* Vachon, 1949 from Iran (Scorpiones, Buthidae). Pp. 179–182 in: Fet, V. &

P. A. Selden (eds.). *Scorpions 2001. In memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society.

LOURENÇO, W. R. & M. VACHON. 2004. Considérations sur le genre *Buthus* Leach, 1815 en Espagne, et description de deux nouvelles espèces (Scorpiones, Buthidae). *Revista Ibérica de Aracnología*, 9: 81–94.

LOURENÇO, W. R. & V. R. D. VON EICKSTEDT. 1983a. A propósito da indicação de um neótipo para *Tityus serrulatus* Lutz e Mello, 1922 (Scorpiones; Buthidae). *Memórias do Instituto de Butantan*, 44/45(1980/1981): 181–190.

LOURENÇO, W. R. & V. R. D. VON EICKSTEDT. 1983b. Présence du genre *Microtityus* (Scorpiones, Buthidae) au Brésil. Description de *Microtityus vanzolinii* sp. n. *Revue Arachnologique*, 5(2): 65–72.

LOURENÇO, W. R. & V. R. D. VON EICKSTEDT. 1984. Descrição de uma espécie nova de *Tityus* coletada no estado da Bahia, Brasil (Scorpiones, Buthidae). *Journal of Arachnology*, 12(1): 55–60.

LOURENÇO, W. R. & W. WEITSCHAT. 1996. More than 120 years after its description, the enigmatic status of the genus of the Baltic amber scorpion “*Tityus eogenus*” Menge, 1869 can finally be clarified. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 79: 189–193.

LOURENÇO, W. R. & W. WEITSCHAT. 2000. New fossil scorpions from the Baltic amber - implications for Cenozoic biodiversity. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 84: 247–260.

LOURENÇO, W. R. & W. WEITSCHAT. 2001. Description of another fossil scorpion from the Baltic amber, with considerations on the evolutionary levels of Cenozoic Buthoidea. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 85: 277–283.

LOWE, G. 2000. A new species of *Babycurus* (Scorpiones, Buthidae) from Northern Oman. *Entomological News*, 111: 185–192.

LOWE, G. 2001. A new species of *Compsobuthus* Vachon, 1949 from Central Oman (Scorpiones, Buthidae). Pp. 171–177 in: in: Fet, V. & P. A. Selden (eds.). *Scorpions 2001. In memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society.

MAURY, E. A. & W. R. LOURENÇO. 1987. *Tityus roigi*, nouvelle espèce de scorpion de l'Équateur (Scorpiones, Buthidae). *Revue Arachnologique*, 7(2): 79–84.

PAGE, R. D. M. 1998. *TreeView (win32) 1.5.2*. Glasgow, Scotland.

PINTO-DA-ROCHA, R. & W. R. LOURENÇO. 2000. Two new species of *Tityus* from Brazilian Amazonia (Scorpiones, Buthidae). *Revue Arachnologique*, 13(13): 187–195.

PRENDINI, L. 2000. A new species of *Parabuthus* Pocock (Scorpiones: Buthidae), and new records of *Parabuthus capensis* (Ehrenberg), from Namibia and South Africa. *Cimbebasia*, 16: 31–45.

PRENDINI, L. 2003. Discovery of the male of *Parabuthus muelleri*, and implications for the phylogeny of *Parabuthus* (Scorpiones: Buthidae). *American Museum Novitates*, 3408: 1–24.

PRENDINI, L. 2004a. On the scorpions of Gabon and neighboring countries, with a reassessment of the synonyms attributed to *Babycurus buettneri* Karsch and a redescription of *Babycurus melanicus* Kovařík. *Memoirs of the California Academy of Sciences*, 28: 235–267.

PRENDINI, L. 2004b. Systematics of the genus *Pseudolychas* Kraepelin (Scorpiones: Buthidae). *Annals of the Entomological Society of America*, 97(1): 37–63.

QI, J.-X., ZHU, M.-S. & W. R. LOURENÇO. 2004. Redescription of *Mesobuthus martensii martensii* (Karsch, 1879) (Scorpiones: Buthidae) from China. *Revista Ibérica de Aracnología*, 10: 137–144.

QUIROGA, M., L. DE SOUSA, P. PARRILLA-ÁLVAREZ & J. MANZANILLA. 2004. The first report of *Tityus* (Scorpiones, Buthidae) in Anzoátegui State, Venezuela. A new species. *Journal of Venomous Animals and Toxins including Tropical Diseases*, 10(1): 10–33.

SANTIAGO-BLAY, J. A. 1985a. *Microtityus dominicanensis*: a new scorpion from the Dominican Republic, West Indies (Scorpiones, Buthidae). *Entomological News*, 96(1): 1–6.

SANTIAGO-BLAY, J. A. 1985b. Redescription of *Tityus dasyurus dasyurus* Pocock, 1897 (Scorpiones, Buthidae). *Revue Arachnologique*, 6(2): 49–56.

SANTIAGO-BLAY, J. A., V. FET, M. E. SOLEGLAD & P. CRAIG. 2004a. A second scorpion specimen from Burmese amber (Arachnida: Scorpiones). *Journal of Systematic Palaeontology*, 2(2): 147–152.

SANTIAGO-BLAY, J. A. & G. O. POINAR, JR. 1988. A fossil scorpion *Tityus geratus* new species (Scorpiones: Buthidae) from Dominican amber. *Historical Biology*, 1: 345–354.

SANTIAGO-BLAY, J. A., M. E. SOLEGLAD & V. FET. 2004b. A redescription and family placement of *Uintascorpio* Perry, 1995 from the Parachute Creek Member of the Green River Formation (Middle Eocene) of Colorado, USA (Scorpiones: Buthidae). *Revista Ibérica de Aracnología*, 10: 7–16.

SCHAWALLER, W. 1979. Erstnachweis eines Skorpions im Dominikanischen Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Scorpionida). *Stuttgarter Beiträge zur Naturkunde*, (B), 45: 1–15.

SCHAWALLER, W. 1981. Zwei weitere Skorpione im Dominikanischen Bernstein (Stuttgarter Bernstein-Sammlung: Arachnida, Scorpionida). *Stuttgarter Beiträge zur Naturkunde*, (B), 82: 1–14.

SCOTESE, C. R. 2001. *Atlas of Earth History, Volume I, Paleogeography*. PALEOMAP Project, Arlington, Texas, 52 pp.

SISSOM, W. D. 1990. Systematics, biogeography and paleontology. Pp. 64–160 in Polis, G. A. (ed.), *The Biology of Scorpions*. Stanford University Press, Stanford, California.

SISSOM, W. D. 1994. Descriptions of new and poorly known scorpions of Yemen (Scorpiones: Buthidae, Diplocentridae, Scorpionidae). *Fauna of Saudi Arabia*, 14: 3–39.

SISSOM, W. D. 1995. Redescription of the scorpion *Centruroides thorelli* Kraepelin (Buthidae) and description of two new species. *Journal of Arachnology*, 23(2): 91–99.

SISSOM, W. D. & V. FET. 1998. Redescription of *Compsobuthus matthiesseni* (Scorpiones: Buthidae) from southwestern Asia. *Journal of Arachnology*, 26: 1–8.

SISSOM, W. D. & O. F. FRANCKE. 1983. Redescription of *Centruroides testaceus* (DeGeer) and description of a new species from the Lesser Antilles (Scorpiones: Buthidae). *Occasional Papers of the Museum, Texas Tech University*, 88: 1–15.

SISSOM, W. D. & W. R. LOURENÇO. 1987. The genus *Centruroides* in South America (Scorpiones, Buthidae). *Journal of Arachnology*, 15(1): 11–28.

SOLEGLAD, M. E. & V. FET. 2001. Evolution of scorpion orthobothriotaxy: a cladistic approach. *Euscorpius*, 1: 1–38.

SOLEGLAD, M. E. & V. FET. 2003a. The scorpion sternum: structure and phylogeny (Scorpiones: Orthosterni). *Euscorpius*, 5: 1–34.

SOLEGLAD, M. E. & V. FET. 2003b. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, 11: 1–175.

SOLEGLAD, M. E., V. FET & F. KOVÁŘÍK. 2005. The systematic position of the scorpion genera *Heteroscorpion* Birula, 1903 and *Urodacus* Peters, 1861 (Scorpiones: Scorpionoidea). *Euscorpius*, 20: 1–38.

SOLEGLAD, M. E. & W. D. SISSOM. 2001. Phylogeny of the family Euscorpiidae Laurie, 1896: a major revision. Pp. 25–111 in Fet, V. & P. A. Selden (eds.). *Scorpions 2001. In memoriam Gary A. Polis*. Burnham Beeches, Bucks: British Arachnological Society.

STAHNKE, H. L. 1972. A key to the genera of Buthidae (Scorpionida). *Entomological News*, 83(5): 121–133.

STATHI, I. & W. R. LOURENÇO. 2003. Description of a new scorpion species of the genus *Birulatus* Vachon, 1974 (Scorpiones, Buthidae) from Syria. *Zoology in the Middle East*, 30: 105–110.

SWOFFORD, D. L. 1998. *PAUP\*. Phylogenetic Analysis Using Parsimony (\*and other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.

TERUEL, R. 2000. Una nueva especie de *Microtityus* Kjellesvig-Waering, 1968 (Scorpiones, Buthidae) de Cuba oriental. *Revista Ibérica de Aracnología*, 1: 31–35.

TERUEL, R. 2001a. Redescripción de *Alayotityus delacruzi* Armas, 1973 (Scorpiones, Buthidae). *Revista Ibérica de Aracnología*, 3: 17–24.

TERUEL, R. 2001b. Tres nuevas especies de *Centruroides* (Scorpiones, Buthidae) de Cuba. *Revista Ibérica de Aracnología*, 3: 93–107.

TERUEL, R. & S. A. STOCKWELL. 2002. A revision of the scorpion fauna of Honduras, with the description of a new species (Scorpiones, Buthidae, Diplocentridae). *Revista Ibérica de Aracnología*, 6: 111–127.

VACHON, M. 1940a. Voyage en A.O.F. de L. Berland et J. Millot. Scorpions. V. *Bulletin de la Société Zoologique de France*, 65: 170–184.

VACHON, M. 1940b. Sur la systématique des Scorpions. *Mémoires du Muséum National d'Histoire Naturelle, Paris*, 13(2): 241–260.

VACHON, M. 1950a. Quelques remarques sur le peulement en Scorpions du Sahara à propos d'une nouvelle espèce du Sénégal: *Butheolooides monodi*. *Bulletin de la Société Zoologique de France*, 75(4): 170–176.

VACHON, M. 1950b. Subsídios para o estudo da biologia na Lunda. Remarques sur les scorpions de l'Angola (Première note). *Publicações Culturais da Companhia de Diamantes de Angola (Luanda)*, 1950: 5–18.

VACHON, M. 1952. *Etudes sur les Scorpions*. Institut Pasteur d'Algérie, Alger, 482 pp.

VACHON, M. 1958. Scorpionidea (Chelicerata) de l'Afghanistan. The 3rd Danish Expedition to Central Asia. (Zoological Results 23). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København*, 120: 121–187.

VACHON, M. 1960a. Quelques remarques sur *Apistobuthus pterygocercus* Finnegan, Scorpion (Buthidae) habitant l'Arabie. *Archives de l'Institut Pasteur d'Algérie*, 38: 399–405.

VACHON, M. 1960b. Quelques remarques sur *Hemibuthus crassimanus* (Pocock 1900), Scorpion (Buthidae) de l'Inde. *Bulletin de la Société Zoologique de France*, 85: 241–245.

VACHON, M. 1961. A propos d'un Scorpion de l'Inde: *Buthoscorpion laevicauda* Werner (Famille des Scorpionidae) synonyme de *Stenochirus politus* Pocock, 1899 (Famille des Buthidae). *Bulletin de la Société Zoologique de France*, 86: 789–795.

VACHON, M. 1969. *Grosphus griveaudi*, nouvelle espèce de Scorpion Buthidae malgache. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, (2), 41: 476–483.

VACHON, M. 1972. Remarques sur les Scorpions appartenant au genre *Isometrus* H. et E. (Buthidae) à propos de l'espèce *Isometrus maculatus* (Geer) habitant l'île de Paques. *Cahiers du Pacifique*, 16: 169–180.

VACHON, M. 1974. Étude des caractères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en Arachnologie, Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, (3), 140 (Zool. 104), mai–juin 1973: 857–958.

VACHON, M. 1975. Sur l'utilisation de la trichobothriotaxie du bras des pédipalpes des Scorpions (Arachnides) dans le classement des genres de famille des Buthidae Simon. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, (D), 281(21): 1597–1599.

VACHON, M. 1976. *Isometrus (Reddyanus) heimi*, nouvelle espèce de Scorpion Buthidae habitant la Nouvelle-Calédonie. *Cahiers du Pacifique*, 19: 29–45.

VACHON, M. 1977. Contribution à la connaissance de la trichobothriotaxie chez scorpion cavernicole *Alayotityus delacrui Armas* 1973 (famille des Buthidae), suivie de quelques données biospéologiques. In T. Orghidan, A. Nunez Jimenez et al. (eds.) *Résultats des expéditions biospéologiques Cuba-no-Roumaines à Cuba*. Bucharest: Institut de Spéléologie "Emil Racovitză", 2: 93–97.

VACHON, M. 1979. Notes on the types of scorpions in the British Museum (Natural History), London. *Buthus socotrensis* Pocock, 1889 (Family: Buthidae). *Bulletin of the British Museum, Natural History (Zoology)*, 36(4): 233–237.

VACHON, M. 1982. Les scorpions de Sri Lanka. (Recherches sur les scorpions appartenant ou déposés au Muséum d'Histoire naturelle de Genève III). *Revue suisse de Zoologie*, 89(1): 77–114.

VACHON, M. 1986. Étude de la denture des doigts des pédipalpes chez les Scorpions du genre *Lychas* C. L. Koch, 1845 (Arachnida, Scorpiones, Buthidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, (A), 8(4): 835–850.

VENCES, M., J. FREYHOF, R. SONNENBERG, J. KOSUCH, & M. VEITH. 2001. Reconciling fossils and molecules: Cenozoic divergence of cichlid fishes and the biogeography of Madagascar. *Journal of Biogeography*, 28: 1091–1099.